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MATHEMATICAL MODELING OF THE GROWTH AND DEVELOPMENT OF POTATOES (*Solanum tuberosum* L.)

BY

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By

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March 1980

Chairman: Darell E. McCloud
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During the 1978 growing season a growth analysis was performed on potatoes (Solanum tuberosum L.) planted on 2 February and 14 March. Two cultivars, Monona and Sebago, were studied. During the winter of 1979 a thermogradient analysis of Sebago growth was conducted. The objective of these studies was to provide data for the development and validation of a mathematical crop growth and development model. During the summer and fall of 1979 such a crop model was written in the GASP IV simulation language. The purpose of the crop model was to elucidate the effects of temperature on assimilate partitioning.

The results of the crop growth and development model indicated that the primary effect of soil temperature was through a direct regulation of the tuber growth rate which had a 15° C temperature optimum. A high potential tuber growth rate stimulated photosynthesis; so a secondary effect of soil temperature was on net daily photosynthesis.

The major effect of air temperature was its influence on the tuber initiation date. Air temperature and tuber initiation rate were inversely related. The air temperature also affected the rate of canopy senescence with warm temperatures speeding leaf drop and reducing the crop growth rate. The main weakness of the model was that light interception data were input rather than generated by the model itself.

INTRODUCTION

There are four factors which determine a crop's yield: 1) the rate of crop photosynthesis; 2) the amount of assimilate which can be mobilized and translocated to the yield component from storage in other crop organs; 3) the portion of daily photosynthesis deposited in the yield organ; and 4) the duration of yield organ growth. Of these yield determining factors, the daily photosynthate partitioning and the length of the yield organ growth period show most potential response to manipulation for increasing yields. The mechanisms which regulate photosynthate distribution are not clear; so it is impossible to systematically change partitioning *per se*.

It is the aim of this study to elucidate the effects of temperature on photosynthate partitioning. The potato, *Solanum tuberosum* L., was chosen as the experimental subject because the yield organs and the photosynthetic organs grow in different thermal environments. The soil temperature of the tuber environment has smaller amplitude of fluctuation and different times of maximum and minimum temperatures than the aerial temperatures of the crop canopy. Further, these thermal differences occur on both daily and seasonal bases.

In field and greenhouse studies many other environmental factors confound interpretation of thermal effects. Therefore, a computer simulation model was developed to isolate thermal effects on potato crop growth dynamics.

LITERATURE REVIEW

Eco-Physiological Crop Modeling

Agronomists often use the terms crop ecology and crop physiology synonymously. This confusion stems partly from the fact that ecology and physiology are terms which originate from studies of natural biological systems. Ecology can be defined as the study of relationships between organisms and their environment. Physiology is the study of normal functioning of organisms and their organs. When applied to crop systems these definitions overlap. The goal of crop physiology is to better understand the dynamics of yield development (Evans, 1975a). Crop physiology greatly depends upon environmental factors which are the subject of ecology. Milthorpe and Moorby (1974) use the term physiology when considering interrelationships between crop plants and abiotic environmental factors as well as competitive interactions between higher plants comprising the crop system. Some authors recognize the commonalities between the two fields of study by using the terms eco-physiology (Eckard, 1965) or ecological physiology (Leopold and Kriedemann, 1975).

This eclectic area is fundamental to models of crop growth and development. Crop models attempt to mathematically describe plant responses to environmental inputs. The models most frequently encountered in literature tend to minimize input variables and responses to facilitate understanding of the model. For example, Lynch and Rowberry (1977a) tested two reciprocal polynomial models

to determine which best described the relationship between potato stem density and tuber yield. They used the single input, stem density, to predict two responses, total tuber yield and marketable tuber yield. More complex models have been developed to describe other crop system phenomena. Several models have been published which describe soil-plant water relationships (Campbell et al., 1976; De Vries, 1972), crop photosynthesis (Duncan et al., 1967; De Wit, 1959), and crop microclimate (Goudriaan and Waggoner, 1972). In fact, any mathematical description which relates two or more factors, such as by regression analysis, is a model. With the advent of high speed computers the art and science of modeling have progressed from simple statistical type models, to multiple linear regression models, to complex systems of equations which attempt to simulate crop growth and development throughout a growing season and to models of entire eco-system functioning (Stewart, 1975). Moorby and Milthorpe (1975) have published a flow diagram for a possible potato growth model. The complete mathematical description of potato growth and environmental relations is complicated by the enormous range of adaptability and plasticity of the potato crop, the multiplicity of uses to which potatoes are put, and by an incomplete understanding of potato growth physiology.

Similar to ecology and physiology, crop growth and development are often poorly distinguished. Growth, as used here, refers to the increase in dry weight. Development, on the other hand, refers to the combination of organ differentiation and growth coordination. The growth of a crop is highly dependent upon its developmental phase or phenophase. The eco-physiological model must be able to follow growth and development along separate but interdependent time courses.

Crop growth models generally include four primary processes: water relations, mineral uptake and metabolism, photosynthesis, and crop development. The major environmental inputs to these processes are soil nutrient availability, air temperatures, solar radiation, and precipitation or irrigation. The modeler must consider not only the environmental inputs, but also how the particular crop responds to these environmental factors. The purpose of this review is to elucidate some of the more important eco-physiological interrelationships affecting potato crop growth and development.

Crop Phenology

Crop phenology is the study of developmental phenomena which respond to annually periodic environmental stimuli. These developmental phenomena are catalogued by visible morphogenic changes such as bud break, flower initiation, and fruit abscision. Phenology can be contrasted with ontology. While phenology is the study of life cycle changes due to annual climatic fluctuations, ontology is the study of developmental phases through the life of an individual organism (Larcher, 1975). For annual plants the difference between phenology and ontology is slight. Cultivated potatoes fit best in the annual growth habit classification. One might distinguish between potato ontogeny and phenology. The ontogenic cycle begins when the tuber bud is initiated and ends when the canopy produced by that bud senesces. By contrast, the phenologic cycle runs from planting through harvest and storage. Thus ontogenic generations overlap during the period from tuber initiation to harvest while phenologic cycles do not

overlap. Further, phenology emphasizes environmental effects on crop development while ontology tends to focus on genetic factors.

One list of the climatically regulated phenophases in a potato crop's development might include: a) tuber dormancy; b) bud break and shoot elongation; c) root system, rhizome, and canopy development; d) flowering; e) tuberization; f) tuber growth; g) canopy senescence; and h) crop maturity. This list is little more than the organogenic sequence through the crop season. Much more interesting than the phenologic description are the factors which regulate the length of the phenophases.

Heat

The relationship between crop development rates and thermal environment has been noted for many crops. The heat unit theory by Abbe states that plant development depends upon cummulative heat exposure rather than time per se (McCloud, 1979). The national weather service provides growing degree day data in their Weekly Weather and Crop Bulletin to help researchers and growers estimate crop development rates. Most crop models include a subroutine which integrates temperature inputs in order to regulate crop phenology. In fact, for many crop models, heat accumulation alone is sufficient to monitor the crop development rate.

For most crops, development rate and temperature are positively related over the temperature range for normal growth. In wheat, higher temperatures reduce the length of both vegetative and filling phases (Spiertz, 1974). In field work supporting their cotton morphology model Hesketh et al. (1972) found that higher temperatures reduced days from planting to full cotyledon expansion, days between

development of successive leaves on the same branch and between successive branches on the main stem as well as between flowers on a branch. Their work showed that the cummulative heat concept can be used to describe organogenesis, i.e., plastochron duration, as well as longer term phenologic development, i.e., the canopy development phase. Haun (1975) used multiple linear regression to analyze relationships between daily maximum and minimum air temperatures as well as other climatic data with development rate of potato leaves. He found the best correlation between the leaf development rate and temperature when a one or two day lag time for air temperature was used. Unfortunately, since Haun used multiple linear regression analysis, it is nearly impossible to isolate the exact temperature verses development rate relationship.

According to Van Dobben (1962), the effect of heat on the rate of vegetative crop development is independent from the effect of heat on crop growth. Generalized trends of the influence of heat on potato development are as follows: 1) The emergence rate is accelerated at higher temperatures over the range of 12 to 24° C. 2) The optimum temperature for tuberization is around 20° C with initiation delayed relatively more by higher than lower temperatures. At 30° C tubers may never form. 3) At high temperatures the canopy may continue to develop past flowering under conditions of high nutrient availability. Extended canopy growth at high temperatures is likely related to delayed or decreased tuberization which makes more assimilate available for canopy growth (Bodlaender, 1963).

In the above discussion little distinction was made between the relative influences of air and soil temperatures. These factors are

highly correlated and difficult to distinguish (Nielson and Humphries, 1966; Richards, 1952). Richards reported a phase delay and amplitude reduction in the soil temperature with increased depth. In other words, the difference between maximum and minimum temperatures declines with depth, and the time of these maximum and minimum temperatures is delayed. In the root and tuber growth zone, however, the phase shift and amplitude dampening with depth are slight.

In their research on tomatoes, Abdelhafeez et al. (1971) found that the main effect of soil temperature on development rates occurred during the emergence phase. Two weeks past emergence, little distinction could be made between soil temperature treatments. Furthermore, soil temperature had no apparent effect on fruit maturity dates. Still, the findings of Abdelhafeez et al. agreed with those of Nielson and Humphries that soil temperature had a marked effect on root morphology and development. At cool temperatures roots develop more slowly, have fewer secondary roots and become thicker than at higher temperatures.

Soil temperature has an effect on corn development well beyond emergence. Mederski and Jones (1963) found that corn plants grown on soil heated from planting to maturity and from emergence to maturity both reached maximum height earlier and matured earlier than unheated control plants. If, as suggested by Van Dobben (1962), the effect of soil temperature is positively related to the size of the crop propagule's reserve of substrate, then we would expect significant effects of temperature on potato development. Indeed, higher soil temperatures have decreased the time from planting to emergence (Moorby and Milthorpe, 1975). Further, since the tuber of the potato develops underground we might expect that soil temperature plays a

greater role in determining potato crop development than in crops where the bulk of the biomass is aerial. Higher soil temperatures seem to shorten the tuber initiation period with fewer tubers being set. However, the higher soil temperature does not appear to hasten canopy senesence when air temperatures are held constant. Under these conditions, the few tubers which do set at high soil temperature generally grow to larger proportions than tubers growing in cool soil (Bodlaender, 1963; Hagan, 1952b).

The cummulative heat models mentioned above commonly assume a linear form (Figures 1 and 2). The rate of development increases linearly above some base temperature. The development rate may or may not have an upper limit. The Growing Degree Day information published by the National Weather Service assumes zero development above 30° C (Figure 2). The simplicity of these linear models makes them most practical for general use. Discrepancies arise when temperatures fluctuate about the base temperature or the maximum temperature. Tyldesley (1978) presented a model to account for these temperature fluctuations (Figure 3). Tyldesley smoothed the angle between the linear model and the axis.

Solar Radiation

Isolating the effects of solar intensity on crop development is difficult. Radiation provides energy for evapotranspiration and temperature changes within the crop canopy (Chang, 1968). The effects of these climatic factors are confounded in most field experiments. Still, Haun (1975) found significant correlations between light intensity and leaf development in potatoes. Effects of low light intensities on plant development have been studied as well. At low

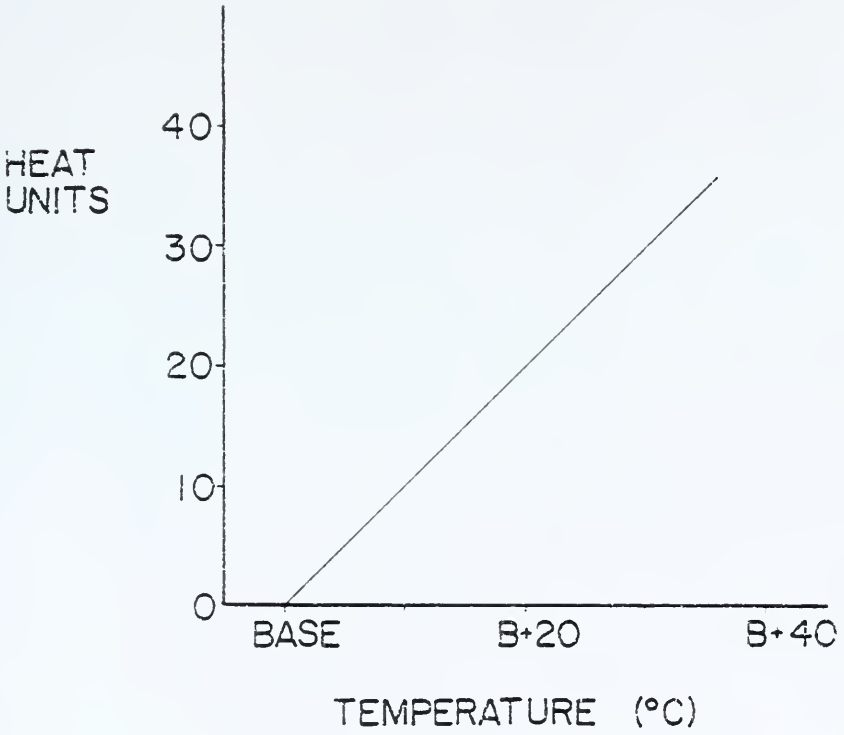

Figure 1. General cummulative heat model with no temperature maximum.

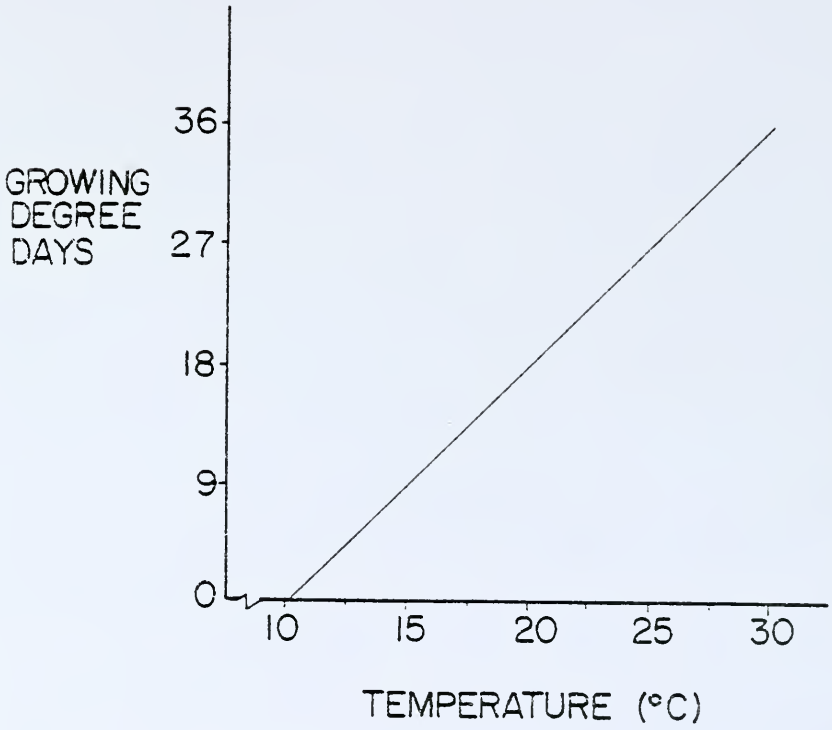

Figure 2. National Weather Service's Growing Degree Day heat model.

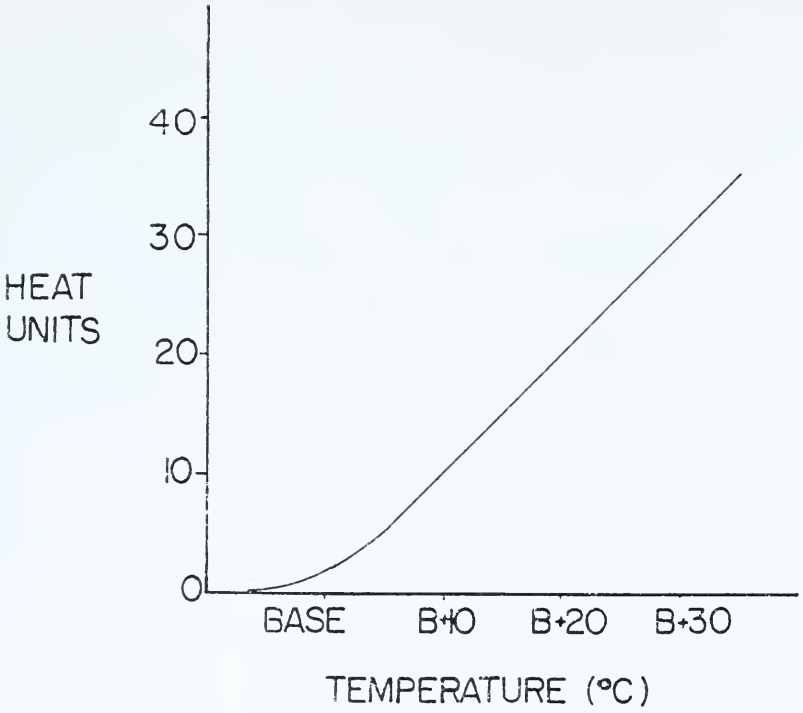

Figure 3. Cummulative heat model which accounts for fluctuations about the base temperature (After Tyldesley, 1978).

light intensities stem elongation is stimulated while leaf development is inhibited (Van Dobben, 1962; Leopold and Kriedemann, 1975). Using potatoes grown at 16 hour days with light intensities from 3,000 to 16,000 lx., Bodlaender (1963) found that the maximum stem length was reached sooner, tubers initiated sooner, the canopy senesced earlier, and flowering was stimulated by the high light level. The applicability of these findings to field conditions is diminished since the highest light intensity was approximately 30% of full sunlight (54,000 lx.). Sale (1973a) found no effect of 21% or 34% shade on the development of field grown potatoes. The plants grown under both of Sale's shade conditions received higher light intensities than those grown in Bodlaender's growth chamber.

Plant breeders have severely altered the photoperiodic response of the potato. Though potatoes were cultivated by Peruvian Indians at least as long ago as 4000 B.C., Spanish explorers did not introduce the potato to Europe until around 1570 A.D. At that time, potatoes were a botanical curiosity. After only 100 years potatoes were grown on a field scale in Ireland. In the same 100 years heavy selection pressure appears to have converted S. tuberosum subspecies andigena, a plant adapted to form tubers under twelve hour days of tropical latitudes, to subspecies tuberosum which initiates tubers under long summer days (Hawkes, 1978). Modern potatoes are classified as either long-day favorable, short-day favorable, or day neutral by Chang (1968). S. tuberosum is one of few species where photoperiodicity is related to tuber formation rather than flowering. The photoperiodic response in potatoes shows great plasticity.

Though some cultivars show more strict photoperiodic responses (Leopold and Kreidemann, 1975), potatoes do not generally exhibit

threshold photoperiodic requirements for tuberization. Rather, photoperiodic classification is based on the effect of photoperiod on the development rate. For example, short-day conditions accelerate progression from one phenophase to the next in European cultivars which are short-day favorable. As well as earlier tuberization, flowers initiate sooner, stem elongation ceases sooner, and plants senesce earlier under favorable photoperiodic conditions (Bodlaender, 1963).

Nutrients

The effect of soil nutrients on potato phenology depends upon timing of fertilizer application. Even the nutrients applied to the seed crop may influence potato phenology. Nitrogen fertilizers applied to the seed crop may hasten maturity in an early crop grown from the seed (Gray,1974). High soil nitrogen levels at the time of planting increase emergence rates (Moorby, 1978). According to Ivins (1963), nitrogen applied during early canopy development will delay tuber initiation and canopy senescence. On the other hand, Dyson and Watson (1971) found that nitrogen fertilization did not delay tuber initiation in King Edward cultivar potatoes. Only zero nitrogen fertilization shortened the period for the canopy to reach its maximum growth. Rather, they found nitrogen to reduce the rate of tuber growth during the period directly following tuber initiation.

Bremner, El Saeed, and Scott (1967) noted sharp inflection points in the graph of tuber:foliage ratio versus total dry weight. These inflection points indicated transition from the vegetative to tuber growth phenophase. Low nitrogen treatments showed significantly faster development according to this analysis. The prolonged canopy

development phase under high nitrogen conditions is associated with an increase in branching rather than main stem growth (Harris, 1978a; Dyson and Watson, 1971).

In their studies with S. tuberosum sp. andigena, the South American ancestor to sp. tuberosum, Ezeta and McCollum (1972) applied three fertilizer levels: 160-160-160; 80-80-80; and 0-0-0 kg/ha of $N-P_2O_5-K_2O_5$, respectively. Potatoes given the low fertilizer treatment matured by 156 days after planting while those given higher fertilizer treatments matured after 172 days. The flowering date was the same for all treatments; so the only apparent effect of high fertility appeared to be to extend the tuber development phase. All of the nitrogen, calcium, and magnesium absorbed by sp. andigena was taken up before tuber initiation. For the more commonly cultivated sp. tuberosum, however, uptake may continue until the beginning of canopy senescence (Soltanpour, 1969). Nitrogen is often taken to be the major nutrient associated with crop development and growth. The relationship between nitrogen level and development or growth is relatively linear over a rather large range of nitrogen levels. Most crops exhibit a threshold type response to levels of other plant nutrients. As long as these nutrients are present above some threshold concentration they have little effect on crop growth or development. Phosphorus and, to some extent, potassium accumulate in soils which are intensively fertilized. Thus, phosphorus and potassium are usually above the threshold. Nitrogen reserves are quickly depleted to suboptimal concentrations in the soil solution (Harris, 1978a).

Dyson and Watson (1971) found potassium to stimulate canopy senescence. Potassium also stimulated the leaf growth rate. Potassium's

combined influences of hastening senescence and leaf growth stimulation give a net zero effect on final yield. McCollum (1978a and 1978b) found that phosphorus applications had opposite effects to nitrogen applications. When phosphorus was applied during canopy development, tuber initiation and canopy senescence were both hastened.

Water

Early irrigation has some effects similar to early nitrogen application on potato development. Both water and nitrogen tend to speed emergence and leaf development while delaying tuber initiation (Sale, 1973b). Unlike nitrogen's effects, however, early irrigation tends to hasten canopy senescence in some potato cultivars (Ivins, 1963; Harris, 1978b). If irrigation is applied soon after tuber initiation the tuber development phase is prolonged and canopy senescence is delayed (Ivins, 1963).

Drought generally has the opposite effect of irrigation. Early drought will cause earlier curtailment of leaf and branch development. This drought effect reflects a reduction in numbers of branches and leaves formed with relatively no change in the rate that new leaves and branches are produced. A short drought period will decrease the development rate of previously initiated leaves in potato plants having tubers but not in pre-tuberous plants. In other words, the rate of unfolding and expanding may be slowed by drought in tuber bearing plants but not in tuberless plants. In both cases, the production of new leaves occurs at the same rate but stops sooner under drought conditions (Munns and Pearson, 1974).

During the tuber growth phase a short drought may retard or stop tuber development. Upon relief from the water stress only the

acropetal tuber tissues resume growth and development. Misshapen tubers result (Moorby et al., 1975; Morby, 1978). These deformed tubers, called second growth tubers, result from rapid maturation of the basipetal tuber buds and adjacent tissues. Since these tissues mature during the stress period only the acropetal buds may resume growth. If all buds in a tuber mature as the result of a short water stress period, the rhizome may resume growth when the stress is removed to give a chain of tubers. Thus, there appears to be a threshold level of tuber and bud development. Buds beyond the threshold level of development rapidly mature and cease growth when stressed and then unstressed. Less well developed buds will continue more or less normal development after the stress period. Long and Penman (1963) reported that resumption of crop growth after drought relief did not occur for several days. They postulated that new roots needed to grow before the recently added soil moisture could be exploited.

Season

The preceding discussion shows that potato phenology is regulated by a complex of environmental factors. The effect of growing season on potato phenology results from interactions between several of the factors. According to Moorby and Milthorpe (1975), potato growing regions may be classified as cool-temperate or warm-subtropical. The cool-temperate production season is limited by frost at both planting and harvest. The warmer subtropical production areas may have two growing seasons per year: the first from the last winter frost to high temperatures of summer; the second after peak summer temperatures until first frost in the fall. One might consider another ecosystem of potato production, the high altitude tropical region. The andigen

subspecies is primarily grown in this region. The literature reviewed pertains to the tuberosum subspecies so the high altitude tropical production region is not included.

The effect of season on potato phenology begins with the soil temperature influence on emergence. The two seasons of production in subtropical areas are at opposite ends of this relationship. The first crop is planted when soils are cool. Emergence is slow. Other factors being constant, the second crop shows rapid emergence since it is planted in warmed soils of late summer. In cool-temperate areas, crops at later planting dates may emerge faster due to a combination of warmer soil temperatures and the likelihood that more sprout development has occurred on seed pieces before planting (Bremner and Radley, 1966; Radley, 1963).

Once the crop has emerged, the length of the next phenophase will be determined by the integrated effects of temperature, photoperiod, nutrition, and water status. Only temperature and photoperiod are necessarily related to season since both water and nutrients may be applied or withheld by the grower. The effects of these two environmental stimuli, temperature and photoperiod, may be superimposed on the effect of the age of the rhizome apex.

The end of the canopy development phase is marked by overlapping commencement of tuber growth, flower initiation, and cessation of leaf and branch growth. Moorby (1978) postulated two control mechanisms for tuber initiation. One is hormonal. Photoperiodic effects on tuberization are likely mediated by phytochrome. Such a phytochrome mechanism would be an example of hormonal regulation of tuber initiation. The other control mechanism Moorby suggested is

substrate mediated. Retardation of canopy growth by low temperatures might allow more assimilates to be translocated to rhizomes to stimulate tuber growth. In some cultivars the canopy growth itself may regulate tuberization. In this case, tubers initiate when a threshold canopy development level (as measured by LAI) is reached (Radley, 1963).

In a cool-temperate region, Bremner and Radley (1966) found that later planted crops had longer canopy development phases than early planted potatoes. These observations conform to the predictions of both of Moorby's tuberization control mechanisms since the later planted potatoes grew in warmer weather and longer days. Sale's (1973a and b) data from Australia's two crop periods can also be explained in terms of the two control mechanisms. Cool temperatures and short days during the first crop season stimulate tuberization more quickly than the warm long days under which the second crop's canopy developed (Moorby and Milthorpe, 1975).

Regardless of the factors which stimulate tuber initiation, the balance of crop growth shifts from canopy to tubers at this time. Known plant growth regulators and a hypothetical tuber forming substance have been implicated with the environmental stimuli mentioned above. As yet, little consensus has been reached. Moorby (1978) declared that the mass of apparently contradictory evidence illustrates the futility at the present time of trying to give any definitive explanation of the mechanism of tuber initiation.

By the time the tuber growth and development phase begins many factors have possibly already contributed to canopy senescence and crop maturity. Plants demaged by frost during early canopy development

appear to senesce earlier than unfrosted plants (Radley, 1963). Further, the lengths of the canopy development and tuber development phases are positively related. A long canopy development phase leads to a long lasting canopy and a long tuber growth phase (Bremner and Radley, 1966; Radley, 1963). According to Radley, the planting date in cool-temperate regions had little influence on senescence time in some of the cultivars tested. Presumably, the effect of canopy size at tuberization on the length of the tuber growth period was overridden by environmental factors.

Crop Growth

The definition of growth as an increase in dry weight is convenient to crop modelers. Dry weight increase can be easily described mathematically as a function of physiologic and phenologic factors. Dry weight increase, of course, is not an inclusive definition of growth. Both popular and scientific connotations of growth include reproduction, enlargement and cell division as well as assimilation (Hagan, 1952a). Crop growth is the result of all of these processes. Thus growth analysis by periodic harvest becomes a powerful instrument for describing these growth phenomena (Radford, 1967; McKinion et al., 1974). Combined with environmental descriptions, growth analysis is a good test of mathematical crop growth models (Leopold and Kriedemann, 1975).

As there are many definitions of growth, there are many ways to label crop growth stages. Growth stages may be associated with the cummulative crop growth curve. The expansion (exponential), linear, and maturation growth stages combine to form a roughly sigmoidal

growth curve which applies to both crop and organ growth (Milthrope and Moorby, 1974; Leopold and Kriedemann, 1975).

Combining the growth of crop organs into total crop growth is the purview of photosynthate partitioning. For seed bearing crops, partitioning may be defined as the division of daily assimilate between reproductive and vegetative plant parts (Duncan et al., 1978). For potatoes, we define partitioning with respect to tuber versus non-tuber plant parts. This poorly understood phenomenon has been related to source-sink strengths (Edelman, 1963), nutrient availability (Alberda, 1962), plant growth regulators (Bruinsma, 1962), and the climatic factors discussed below: heat, PAR, nutrients, and water (Brouwer, 1962a). No single mechanism fully explains assimilate partitioning. Most source-sink arguments are too polarized. Assimilate metabolism and photosynthesis have mutually regulatory feedback. Translocation, the means of this feedback, must be considered in any partitioning scheme as well as the strength of source and sink (Evans, 1975b).

In potatoes the rate of photosynthesis after tuber initiation seems largely determined by tuber growth, the major photosynthate sink (Nosberger and Humphries, 1965). Photosynthesis may increase seven-fold after tuber initiation (Evans, 1975b). Thus tuber presence seems to favor growth. Whether this effect is best explained by source-sink, growth regulator, or nutrient balance remains to be seen.

Heat

As stated above, crop yield is determined by mutually independent temperature effects on growth and development. Van Dobben (1962) further stated that the temperature effect on the crop growth rate is

greater than the temperature effect on development. Where models relating temperature and development are generally linear (Figures 1, 2, and 3), growth and temperature exhibit non-linear relationships (Figures 4, 5, and 6). Crop and organ growth have minimum, optimum, and maximum temperatures called cardinal temperatures. These cardinal temperatures depend upon crop nutrition, solar radiation, and water relations as well as the genotype (Bodlaender, 1963).

A common growth versus temperature model is the Q_{10} notion. For maize seedlings, the Q_{10} was calculated to be greater than three at low temperatures, from three to two at suboptimal intermediate temperatures, and less than one for supraoptimal temperatures (Hagan, 1952a).

Tyldesley (1978) presented several means of modeling non-linear temperature responses. One is a simplified account of the Ontario Heat Unit system (Figure 4). Tyldesley's account assumed the response rate to be parabolic with the optimum rate at 30° C and zero rates at 10 and 50° C where temperatures refer to daily maxima. This heat unit system gives one means of modeling temperature responses which show a definite optimum.

The derivations of two temperature response curves are shown in Figures 5 and 6. Figure 5 is derived from biochemical studies of enzyme catalyzed reactions (Conn and Stumpf, 1972). The three curves represent: i) the temperature response at a constant enzyme activity; ii) the effect of temperature denaturation on enzymatic response; and iii) the overall temperature response of the reaction which is the product of curves i and ii. The shape of curve iii corresponds well

with the temperature response curves published for several crops (Rickman et al., 1975; Hagan, 1952a; Blacklow, 1972; Moorby and Milthorpe, 1975).

Figure 6 shows the difference between the photosynthesis and respiration temperature responses (Larcher, 1975). The dark respiration rate is markedly temperature sensitive. The relationship was found to be exponential over the 6 to 32° C temperature range encountered by Sale (1974) in experiments with Sebago cv. potatoes. The stimulatory effect of high temperature on respiration may be overridden by substrate defficiency, enzyme denaturation, or by respiratory product accumulation with negative feedback control (Hagan, 1952a). Notice that the curves for photosynthesis and respiration both have the shape of curve iii in Figure 5. The similarity of these curves is expected since both photosynthesis and respiration are enzymatic reactions, or more properly, systems of enzymatic reactions.

Sale (1974) discovered a lack of photosynthetic temperature response by a potato canopy. Sale's finding may merely point out that photosynthesis is itself the result of two enzymatic systems having different optimum temperatures, i.e., photosynthesis and photorespiration. The combined effects of two such systems would yield a plateau in the temperature response curve. Gross photosynthesis is commonly considered to be temperature insensitive. Since the initial reactions of gross photosynthesis are driven by PAR these steps may be better explained as physical than enzymatic processes. Still, net photosynthesis includes a respiration term to render it undoubtably temperature sensitive.

Several authors have discussed the relative effects of air and soil temperatures. Nielson and Humphries (1966) found that growth is more inhibited by cold soil than cold air temperatures. The water and nutrient uptake upon which canopy growth depends is greatly slowed by cool soil temperatures (Kramer, 1940; Dalton and Gardner, 1978). Sale (1974) could not find a relationship between soil temperature at 10 cm depth and soil respiration. Sale's inability to find a relationship may be because he made his measurements over uncropped, low-organic-matter soil. Bodlaender (1963) reported that 15 to 18° C is optimal soil temperature for potato growth. Cool air temperature may reduce the rate of assimilate translocation to underground plant parts (Hagan, 1952a). By reducing translocation to roots and tubers, air temperature may affect the optimum soil temperature (Nielson and Humphries, 1966).

Heat has a strong effect on photosynthate distribution in the crop system. Roots generally have a lower temperature optimum for growth than do shoots. The shoot to root ratio increases with temperature during canopy development (Van Dobben, 1962). During reproductive growth of wheat, high temperature favors grain growth over shoot growth. In fact, the shoot decreases in dry weight due to respiration and translocation of stored assimilates to the growing grain (Spiertz, 1974). Heat also affects photosynthate distribution through its influence on development. The longer tuber initiation is delayed in potatoes by suboptimal temperatures, the greater canopy growth is achieved before tuberization if nutrients and water are non-limiting (Bodlaender, 1963). The larger the canopy at tuberization the longer the tuber growth period and greater the final yield. Even though

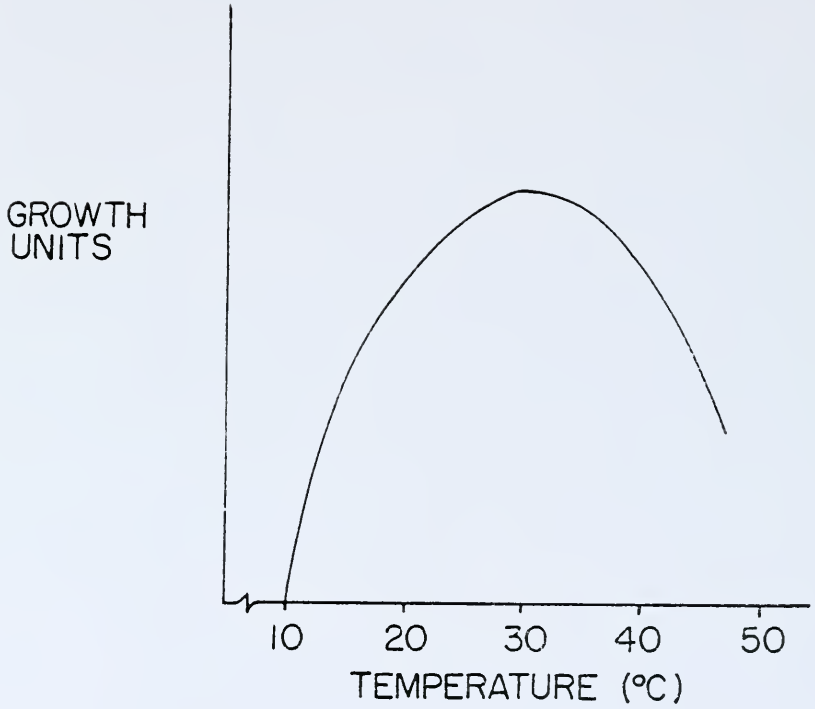

Figure 4. Simplified Ontario Heat Unit System (After Tyldesley, 1978).

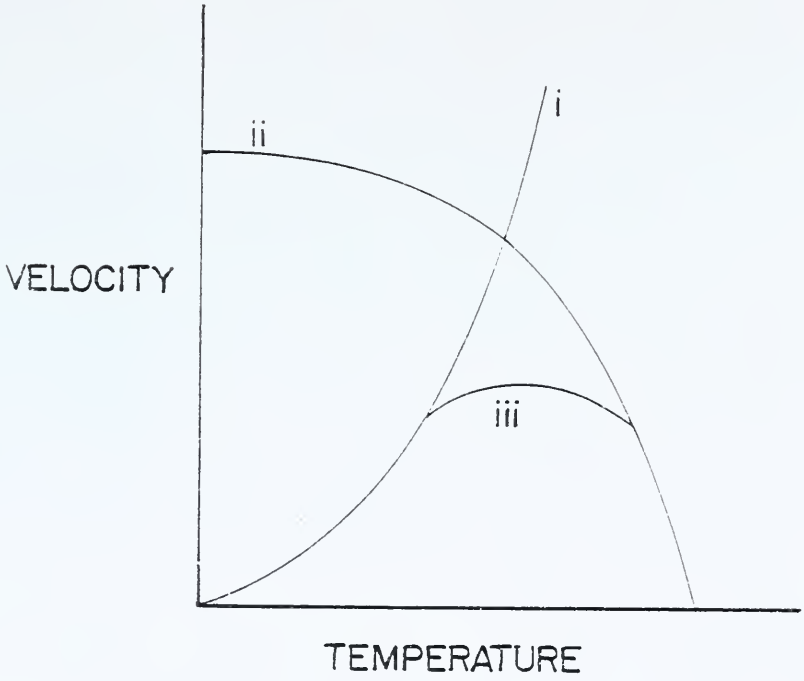

Figure 5. Effect of temperature on the rate of an enzyme catalyzed reaction: i) response with constant enzyme activity; ii) thermal denaturation effect on enzyme activity; iii) reaction rate, the product of curves i and ii (After Conn and Stumpf, 1972).

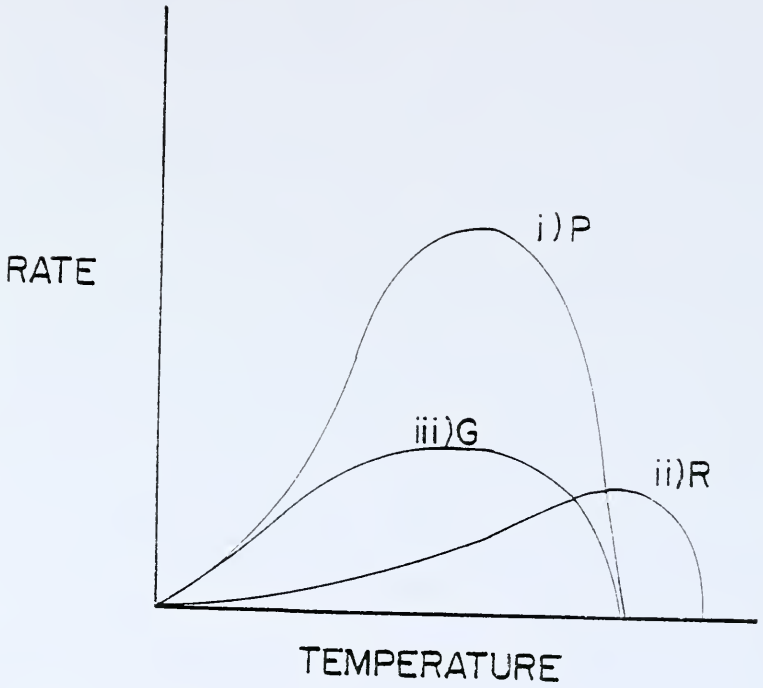

Figure 6. Effect of temperature on: i) Photosynthesis; ii) Respiration; and iii) Growth (After Larcher, 1975).

high temperatures delay tuber initiation, they also accelerate canopy senescence to reduce the tuber growth duration.

Photosynthetically Active Radiation (PAR)

In the previous section, photosynthesis was stated to be relatively temperature insensitive, at least in the primary photoelectric reaction steps. PAR is the driving force for photosynthesis. De Wit (1959) modeled gross photosynthesis as 6.7×10^{-13} g/erg for light intensities below 8.5 ergs PAR/cm^2/sec. Above this light intensity photosynthesis was modeled as a constant 4.7×10^{-8} g/cm^2 (Figure 7). Rijtema and Endrodi (1970) accounted for light intensity effects on growth by estimating the photosynthetic rate under clear and cloudy sky conditions. By measuring daily duration of cloud cover and applying a correction factor to account for canopy ground cover and moisture status Rijtema and Endrodi were able to make fairly accurate predictions of crop growth. Duncan et al. (1967) modeled individual leaf photosynthesis with a rectangular hyperbola. The rectangular hyperbola was also the function derived by Michaelis and Menton to describe enzyme kinetics (Conn and Stumpf, 1972; Thornley, 1976). Using a rectangular hyperbola to model photosynthesis emphasizes the enzymatic underpinnings of photosynthesis (Figure 8). The hyperbolic relationship between light intensity and photosynthesis holds even better for a crop canopy than for an individual leaf (Sale, 1974).

Even though photosynthesis and growth have a positive response to PAR, the efficiency of light utilization declines as light intensity increases. Sale (1973b) reported that photosynthetic efficiency increased as shade was increased from 0 to 34%. Both models, Figures 7 and 8, can explain this finding as both show a decreased

response at high light intensities, i.e., light saturation of photosynthesis. Gaastra (1962) reported that light saturation results when stomata are fully opened at submaximal light intensities. Despite higher efficiency of light utilization at low PAR intensities, yields do increase with higher intensities. Using light levels below one-third full sunlight (92 to 175 cal/cm^2/day), Spiertz (1974) showed that seed yield and growth rates for wheat both increased with light intensity. In maize, Linvill et al. (1978) found highly significant correlations between intercepted solar radiation and grain growth.

In potatoes, light intensity effects assimilate partitioning as well as yield. Shade to 34% had no effect on leaf dry weight although shaded plants had a greater leaf area (Sale, 1973b). The top to tuber ratio increases at lower light intensities (Bodlaender, 1963). In other words, tuber growth, not canopy growth, was reduced by shading. Fewer tubers grew in shaded potatoes though the numbers of tubers initiated and stem density were the same at all light levels tested. The decrease in tuber yield also related to a delay in reaching the maximum tuber growth rate in shaded plants. Delaying the maximum tuber growth rate shortened the tuber growth duration since canopies at all light levels senesced at the same time (Sale, 1973b). Bremner et al. (1967) manipulated interplant competition for light by varying spacing of potted potato plants. More PAR per pot was thereby available at lower densities. The number of stems per seed piece and leaf area per plant remained the same. The LAI was therefore higher at higher densities.

The effect of PAR on the net carbon exchange (NCE) is evident through a diurnal analysis. Sale (1974) reported a mesa-shaped curve

from sunrise to sunset for NCE (Figure 9). He also found that the canopy was light saturated above 400 W/m^2. At this light intensity NCE was approximately 42 mg $CO_2/dm^2/hr$. These PAR effects on growth are moderated by crop age. Stem and leaf respiration declined as the crop matured, probably because growth respiration (as opposed to maintenance respiration) declined. Maximum photosynthesis also declined with crop age. Thus the coefficients in the light response curve equation must be updated through the crop season.

Nutrients

The effects of mineral supply on plant growth are by no means clear. Brouwer (1962b) reported that increased mineral supply leads to a greater increase of shoot than root growth. In fact, Brouwer's data show almost no change in root dry weight over three nitrogen levels in barley plants. Brouwer and De Wit (1968) modeled plant and root growth with low nitrogen supply reducing the shoot to root ratio. This trend was confirmed by Lynch and Rowberry's (1977b) finding that potato root growth was reduced at high fertilizer rates.

These studies considered ratios at a single point in time rather than examining partitioning trends through crop growth. Dyson and Watson (1971) found that even though nitrogen and phosphorus application increased the potato crop growth rate from two to four weeks after emergence, the major effect of the nutrients on growth was through extending the canopy growth period rather than increasing the canopy growth rate *per se*. Similarly, Ivins (1963) found nitrogen applications to increase yield by delaying tuber initiation and extending the tuber growth period.

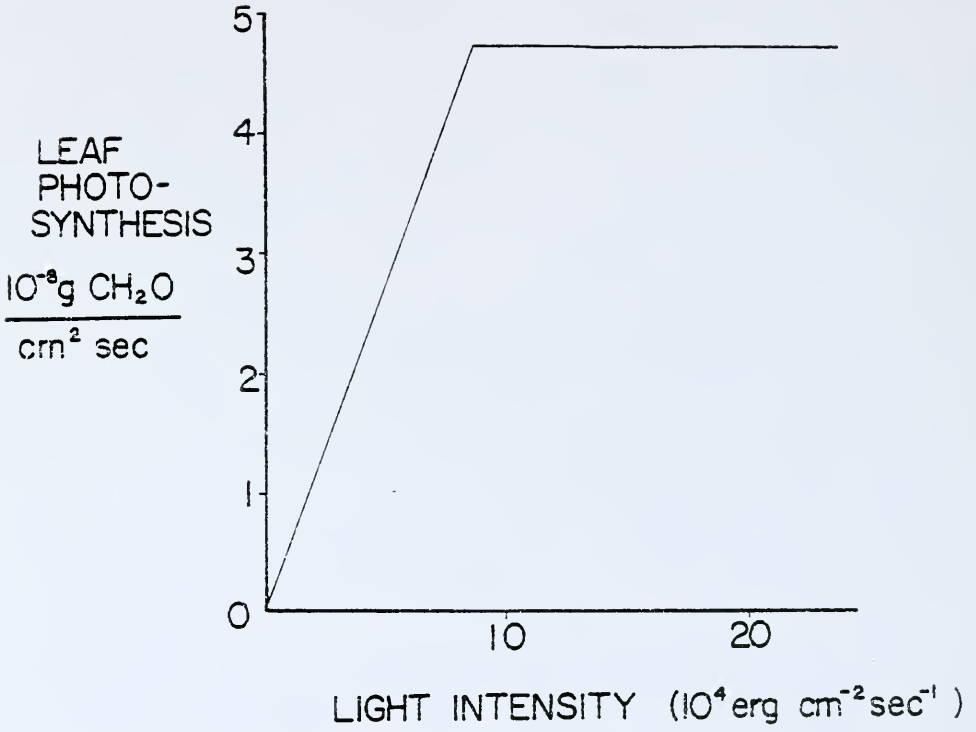

Figure 7. Model of light intensity effect on leaf photosynthesis (After De Wit, 1959).

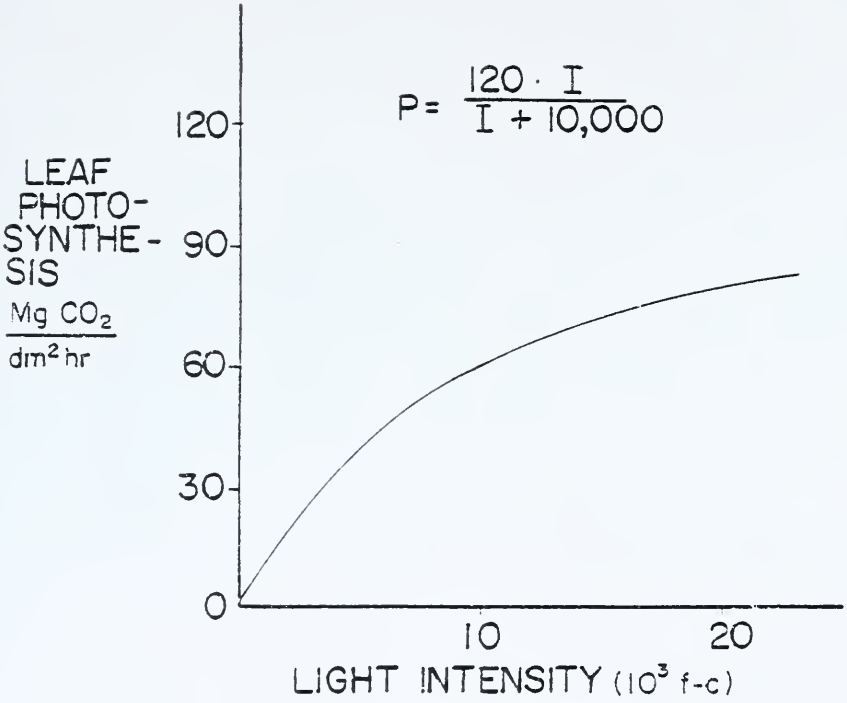

Figure 8. Model of light intensity effect on leaf photosynthesis (After Duncan et al., 1967).

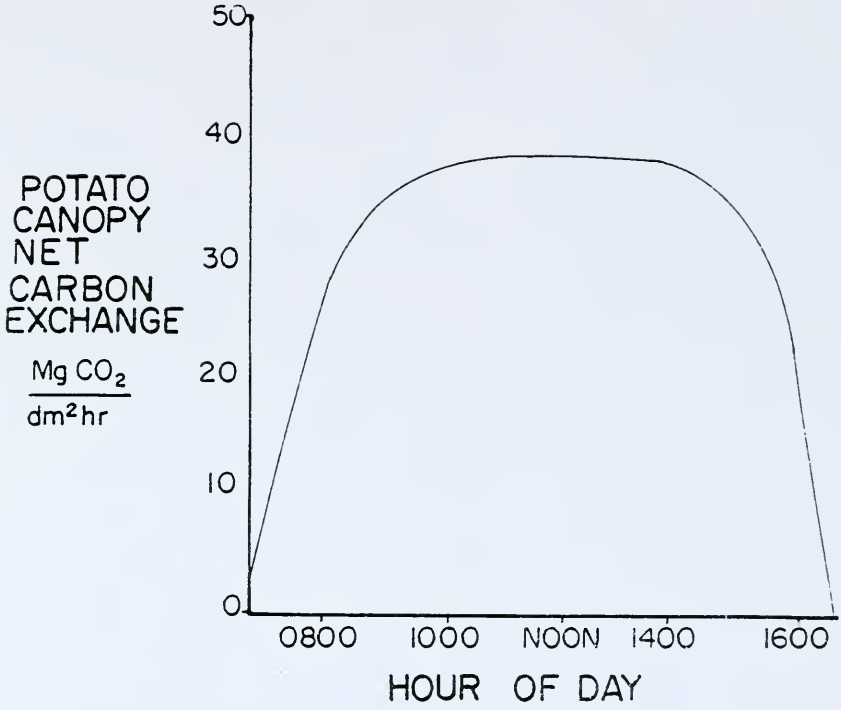

Figure 9. Net carbon exchange in potato canopy from sunrise to sunset (After Sale, 1974).

Nitrogen promotes canopy growth prior to tuber initiation thereby decreasing the tuber to canopy ratio during the early tuber growth period (Dyson and Watson, 1971). By maturity the tuber to canopy ratio in high nitrogen treatments had increased. Thus the nitrogen applications were found to ultimately have increased both tuber and canopy growth.

The effect of nitrogen on tuber yield is limited. Kunkel et al. (1973) found that excess nitrogen will increase canopy growth without affecting tuber yield. Several authors have reported that nitrogen uptake by the potato crop ceases long before tuber growth is complete (Soltanpour, 1969; Ezeta and McCollum, 1972; Dyson and Watson, 1971). After the crop nitrogen uptake ceases nitrogen is apparently translocated from the canopy to the growing tubers. Phosphorus is also translocated from the canopy to the tubers (McCollum, 1978b).

The nutrient concentration in the tubers remains constant through the tuber growth period. Kunkel et al. (1973) reported that the tuber mineral composition was independent of applied nutrient levels or cultural practices. Dyson and Watson (1971), on the other hand, examined tuber carbon to nitrogen ratios and found them to be constant for a given crop but varying between seasons and fertilizer treatments.

All of these findings point toward a mechanism whereby nitrogen regulates tuber growth. Nitrogen levels did not influence the numbers of tubers initiated. Still, Dyson and Watson postulated that nitrogen availability may regulate the tuber sink strength. Of course, during the tuber growth period nitrogen available for tuber growth depends mostly upon the amount of nitrogen in the canopy which is available

for translocation. The more nitrogen in the canopy from increased nitrogen application, the longer the tuber growth period.

Water

Potatoes are generally considered a drought sensitive crop. Drought sensitivity results in part from the potato's relatively shallow root system (Weaver, 1926; Harris, 1978b). Weaver found potato roots to be even less extensive and more shallow when growing under water deficient conditions. Not only do potatoes have shallow roots, but leaf photosynthesis appears to be greatly reduced by a fairly slight reduction in leaf water potential. Campbell et al. (1976) found that stomatal resistance began to increase at a leaf water potential of -0.8 bars. At this level, the effect on crop growth is small. Indeed, Sale (1973a) found that canopy NCE remained relatively constant to leaf water potentials as low as -8.0 bars.

Despite the potato's drought sensitivity, irrigation is not always recommended. In some cultivars, King Edward for example, frequent irrigation during early growth may lead to initiating growth in more tubers. As a result, fewer tubers reach marketable size even though the total tuber yield may increase (Harris, 1978b). Ivins (1963) reported that the number of marketable tubers increased as irrigation was delayed until after linear tuber growth had begun. These reports contrast with Sale (1973a) who found that higher LAI's were reached in potatoes maintained at high soil moisture. Furthermore, the higher LAI's resulted in higher yields due to a longer growth period. Still, there is no dispute that drought during tuber growth will drastically reduce potato yields.

The mechanisms whereby plant water status affects potato yields have been fairly well studied. According to Moorby et al. (1975) leaf sugar concentrations increase in drought stressed potatoes. Drought stress may reduce photosynthate translocation to tubers or reduce starch synthesis within the leaf or both. Munns and Pearson (1974) found that reduction of leaf water potential did indeed decrease translocation of assimilates to tubers, and did so in proportion to its negative effect on net photosynthesis rather than a direct effect on translocation. Thus Munns and Pearson agree with Moorby et al. in finding that drought had no effect on starch synthesizing enzymes in tubers. Tuber growth, or more specifically, tuber starch synthesis appeared to be proportional to assimilate supply and assimilate supply is decreased by drought.

In young potato plants, drought did not seem to influence photosynthate partitioning (Munns and Pearson, 1974). Both canopy and root growth were equally reduced. In older plants, however, drought had less effect on tuber growth than root and canopy growth. Thus the percentage of assimilate partitioned to tubers increased with drought. Drought also more drastically reduced leaf water potential than tuber water potential (Moorby et al., 1975). A mechanism whereby drought may influence partitioning was reported by Necas (1968). During a drought period lower potato leaves abscise. Upon drought relief new leaf area is generated. Since tubers are not shed while leaves are the net effect is an apparent reduction of assimilate partitioned to leaves.

The effect of water status on canopy NCE was also studied by Munns and Pearson. They concluded that drought has a greater negative effect

on NCE of pre-tuberous than post-tuberous plants. The leaf water potentials of young and old plants were not comparable. The young plants had lower leaf water potentials on both stressed and unstressed conditions than did the older plants. Evidently the tubers act as water stores to prevent stress in older plants. Their data show better the effect of leaf water potential on NCE than the influence of tuber presence on NCE in drought conditions.

Density

Since potatoes are propagated vegetatively by tubers, seed expenditures may be as great as 30 to 50% of the total growing costs (Allen, 1978). Thus density effects are of both economic and physiologic importance.

The effects of density on potato crop growth are more complex than the density relationships of most other crops. Units of potato density are several. Allen listed eyes, seed pieces, seed surface area, seed weight, and stems as units of potato density. All of these units are correlated, so all need not be considered in relation to growth. The stem is generally taken as the unit of potato plant density most directly related to yield (Reestman and De Wit, 1959; Bleasdale, 1965; Collins, 1977).

Many factors may influence the stem density. The numbers of stems per seed-piece is positively correlated to the seed-piece weight. This relationship is less notable in cultivars with inherently high stem numbers (Bremner and El Saeed, 1963). Actually, the stem number per seed-piece is more highly related to seed surface area than weight (Reestman and De Wit, 1959), though the effects are difficult to separate. Concomitant with fewer stems in smaller seed-pieces, stems produced from

small seed attained a greater final weight and produced more and larger tubers when planted at the same seed-piece density as large seed-pieces (Bremner and El Saeed, 1963). Thus, the small seed-pieces had a lower stem density.

Similar results were noted by Svensson (1966). He found that LAI, tuber yields, tuber numbers, and mean tuber weights per seed-piece were all higher at wider spacings. As with many other crops, the total tuber yield showed an optimum plateau. Lynch and Rowberry (1977a) measured this optimum density plateau to range from 6 to 12 stems/m^2. Bremner and Taha (1966) found density and tuber growth rate per unit area to be positively related. At higher stem densities a smaller portion of photosynthate is partitioned to tuber growth (Bremner and El Saeed, 1963). Thus, density is one of the few factors which can be easily manipulated to influence tuber growth rates.

Summary

The major dynamic environmental inputs for a potato growth and development model are heat, moisture, nutrients (especially nitrogen), and solar radiation. Other factors may be considered as combinations of these four major inputs or as static, one-time inputs. For example, season may be considered to be a combination of solar radiation and heat effects which change predictably through the year. Crop density, on the other hand, remains relatively constant through the growing season so it need be input only once. The bulk of a crop model, therefore, will describe the relationships between crop growth and the four major inputs.

Prior to tuber initiation, warm temperatures (20-24° C), high available nutrients and water, high PAR flux density, and long days will stimulate and prolong canopy growth. Similarly, cool temperatures, low nutrient and moisture availability, and short days favor early tuber initiation and reduced canopy growth. After tubers have initiated, optimum conditions are soil temperatures from 16 to 20° C, air temperatures from 20 to 24° C, high available nutrients and moisture, and high PAR flux density (Milthorpe, 1963).

MATERIALS AND METHODS

Crop Growth Model

A model was developed to further understanding of how temperature influences crop partitioning. The particular hypothesis to be tested was: differences in the temperature versus growth relationships between various potato organs may be used to predict dry matter distribution within the crop.

The model was tested in the form of a computer program written in GASP IV, a Fortran-based simulation language (Pritsker, 1974). GASP IV has both continuous and discrete simulation capabilities, but the model developed herein is entirely discrete. Features of the GASP IV language crucial to this model are a table search function called GTABL and the language's event filing mechanism.

GTABL calls data from a table array. For example, a table of tuber growth versus temperature can be entered into an array. The GTABL function will derive the tuber growth for a given temperature. The event filing mechanism of GASP IV uses information stored in a buffer called ATRIB(1). ATRIB(1) stores the time an event will occur. ATRIB(2) stores the number of the event which is scheduled for that particular time. ATRIB(3,....,n) can be used to hold any special data required in an event.

The program includes five event subroutines:

1) Pre-tuberous growth (PRET) calculates crop growth and dry matter distribution before the crop initiates tubers, determines when tubers are to be initiated, and schedules canopy senescence.

2) Post-tuberous growth (POSTT) calculates growth and partitioning after tubers are initiated. Both exponential and linear tuber growth are calculated in POSTT.

3) Canopy decline (CANDE) causes a unit of canopy stored in ATRIB(3) to abscize according to heat units accumulated in ATRIB(4).

4) The daily climatic data inputs are read by DAY which also calculates potential net photosynthesis, mean air and soil temperatures, and tuber respiration.

5) Every evening ENDAY is called to store the day's growth calculations for graphic and numeric output of organ dry weights and certain program parameters.

A program listing of this model is included in Appendix A.

The model was validated by inputting actual climatic and ground cover data and comparing the simulated crop growth and development to the results of the growth analysis. To test the effect of temperature on assimilate partitioning and crop growth dynamics a temperature sensitivity analysis was performed.

Growth Analysis 1978

The major objective of the growth analysis was to provide data for the development and validation of the computer model. Planting date was chosen as the most practical means of manipulating temperatures in the field. In keeping with the model purposes, the growth analysis was designed to determine temperature effects on the crop growth rate, tuber growth rate, partitioning, and phenology. Two cultivars were grown in order to compare genetic and environmental effects on potato growth and development.

During the 1978 potato growing season Sebago and Monona cultivars were grown at the Yelvington Experimental Farm of the University of Florida in Hastings. The soil was of the Rutlege taxajunct, now classified as a sandy, silaceous, thermic Typic Humaquept. Crop husbandry was as recommended by the Potato Production Guide (Montelero and Marvel, 1971). Nematodes were controlled by Dichloropropane-Dichloropropene applied two weeks pre-planting at 225 liters/ha. At planting fertilizer was banded at a rate of 120 kg N/ha, 160 kg P_2O_5/ha, and 160 kg K_2O/ha. Between tuber initiation and full ground cover achievement, a sidedressing of 35 kg N/ha and 35 kg K_2O/ha was applied. Weeds were controlled by a 5 kg/ha pre-emergence application of Dinoseb and by cultivation after emergence. Carbaryl and Maneb were applied together at seven to ten day intervals throughout the season as needed for insect and late blight control, respectively. Carbaryl was applied at 1.1 kg/ha and Maneb at 1.3 kg/ha.

Four replicates of both cultivars were planted on each of two dates, 2 February (Julian day 33) and 14 March (Julian day 73). A split plot design was used with planting date comprising the main plot treatment and cultivar the subplot treatment, for a total of 16 subplots. The subplots were 8 by 8.5 m each with rows oriented east-west. The seed-piece spacing was approximately 20 cm within rows and 100 cm between rows giving a density of 4.56 seed-pieces per square meter. The seed-pieces were machine-cut on the first planting date and hand-cut on the second planting date to about 55 g each, giving a seedling rate of 250 g/m^2.

Harvests were taken at seven to ten day intervals through the growing season. Sequential harvests were taken from east to west

within each subplot. Twelve seed-piece clusters (hills) from each subplot were divided into tops, tubers, and remainder which included roots, rhizomes, below ground stems, and seed-pieces. All components were dried at 100° C and weighed. Two representative plants were selected from each subplot and divided into laminae, petioles and midribs, above and below ground stems, inflorescences, rhizomes, roots, tubers, and seed-piece according to the crop's developmental status. Stem length, tuber number, and inflorescence number were all recorded. Leaf area was measured on an electronic area meter. For early samples the entire sample was dried for weighing. At later dates, the total fresh weight was measured and dry weight was determined by subsample. Leaf area was also determined by subsample for later harvest dates.

Environmental data were collected by the IFAS experiment stations in both Hastings and Gainesville, Florida. Measurements used from the Hastings station were daily maximum and minimum air temperature in a standard shelter at 150 cm, daily maximum and minimum soil temperature at 10 cm depth, and precipitation (Figures 10 and 11). From the Gainesville station about 60 miles west of Hastings measurements of daily PAR were used (Figure 12). As well as these standard weather readings, occasional soil temperature profile measurements were made in the experimental plots to compare with the standard data. Diurnal cycles and seasonal trends were observed. Measurements were made at 1, 5, 15, 25, and 40 cm soil depth, and air temperature in the shade of the canopy (Figure 13).

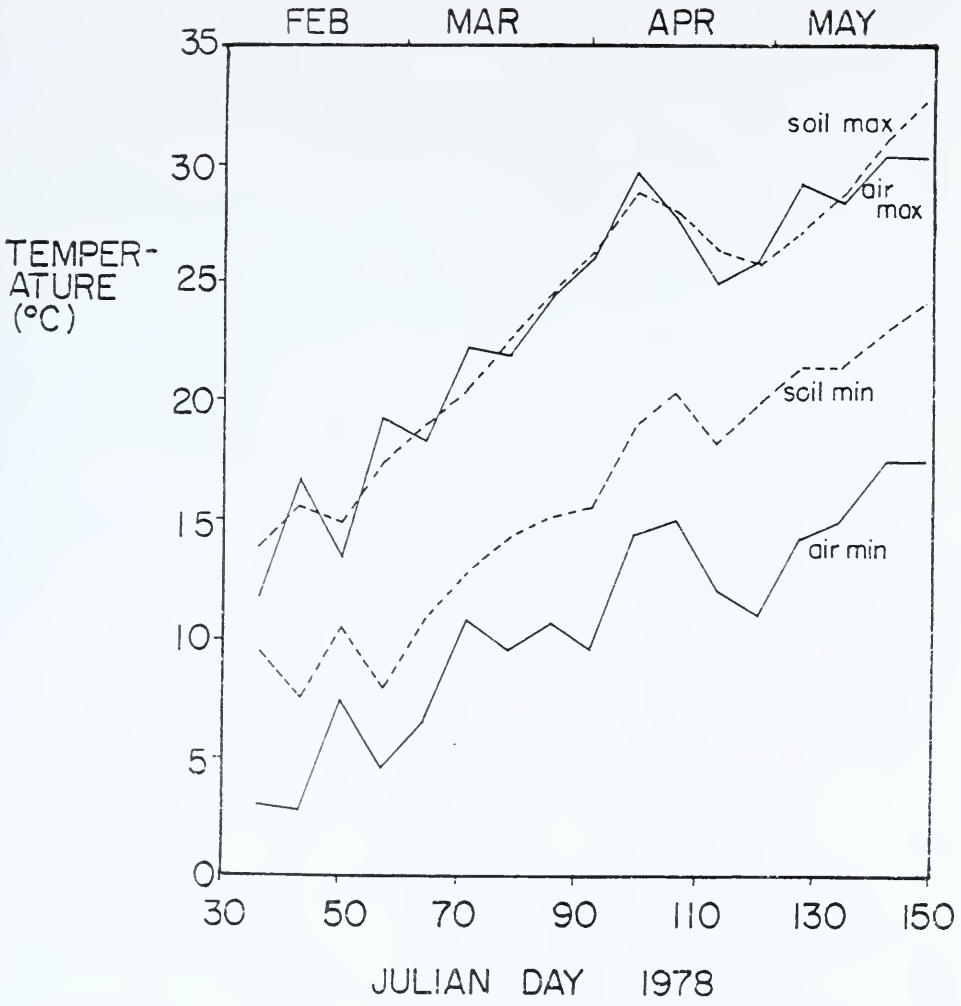

Figure 10. Weekly average temperatures in Hastings, Florida. Air temperatures (——) measured in standard shelter at 150 cm height. Soil temperatures (-----) measured at 10 cm depth.

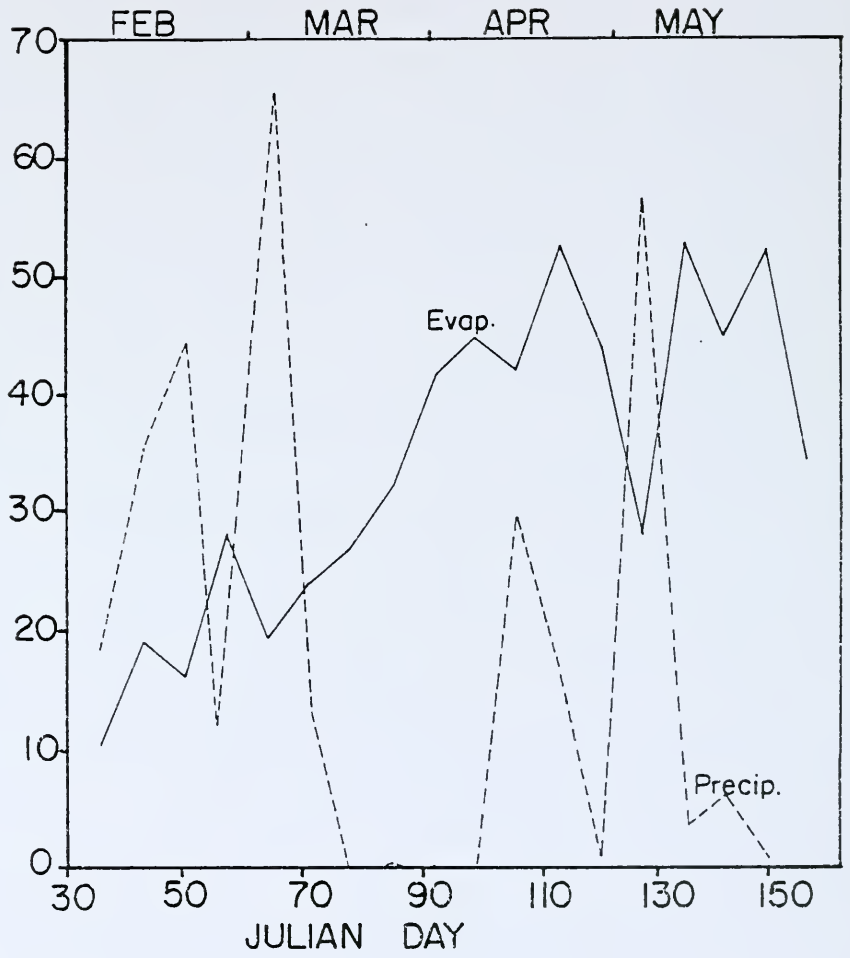

Figure 11. Total weekly precipitation (-----) in Hastings, Florida, and pan evaporation (——) in Gainesville, Florida.

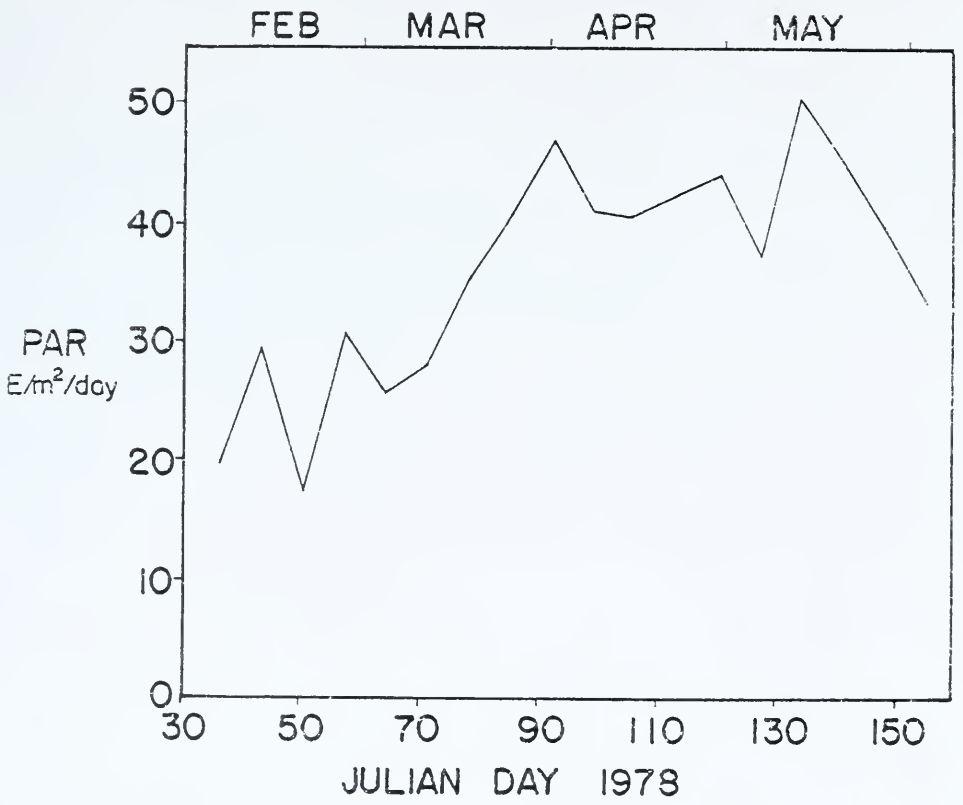

Figure 12. Daily photosynthetically active radiation averaged over one week intervals.

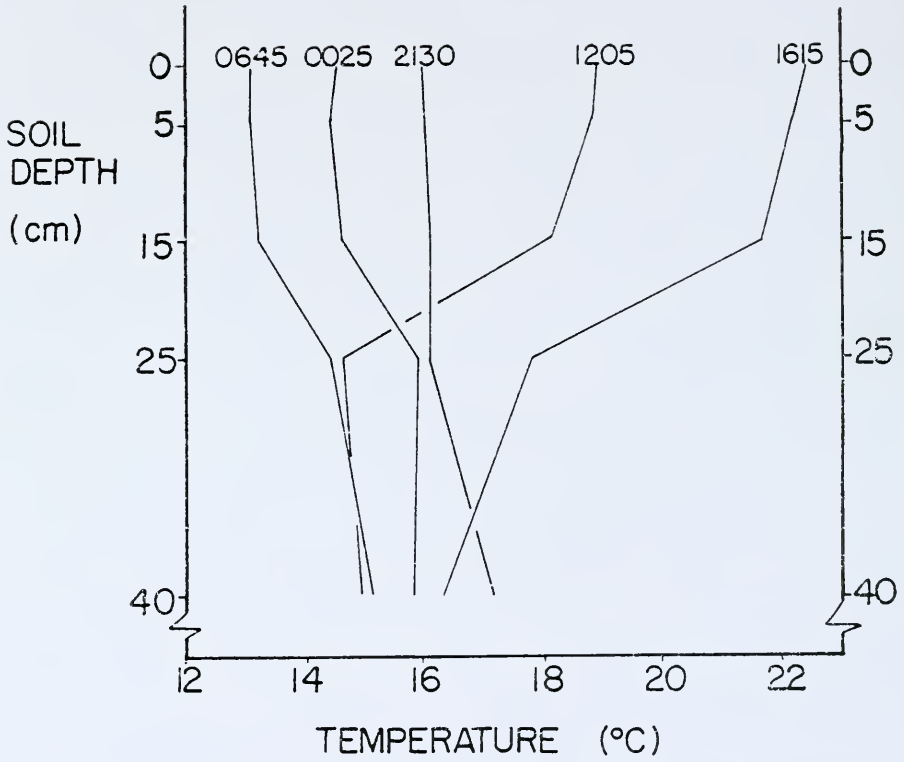

Figure 13. Soil temperature profiles under a Sebago canopy from 1615 hours on March 20, 1978 to 1205 hours on March 21, 1978.

Thermogradient Analysis 1979

The growth analysis considered only two temperature treatments. Though two temperature levels are enough to estimate the general range for model parameters, more temperature treatments are necessary to derive a temperature response curve. Thermogradient analysis was used primarily to determine the shapes for the temperature responses of stem, root, and tuber growth.

During the winter of 1979 a series of experiments was conducted in a thermogradient bath system located at the Biven's Arm Agronomy greenhouse in Gainesville. The thermogradient system, similar to systems used by Kirkham and Ahring (1978) and Timbers and Hocking (1971), was maintained by a water-covered steel bar with one end of the bar emersed in hot water and the other emersed in cold water. All experiments used uncut, grade B, Foundation potato seed of Sebago cultivar. The mean seed-piece fresh weight was 67.5 gm with a standard deviation of 21.2 gm. Table 1 lists dates, temperature ranges, and fresh weight of seed-pieces used in the thermogradient experiments.

To study the effect of temperature on shoot elongation, seed-pieces were planted about 20 cm deep in moist sandy soil held by 0.95 liter paper cups. Convective currents in the gradient bath were reduced by 20 mm polystyrene baffles. Ten baffles divided the thermogradient perpendicularly to form 11 chambers. Each chamber was considered to be at one temperature. Five cups, each containing one seed-piece, were placed in each chamber and all chambers were covered with a polyethylene sheet (6 mil) to prevent evaporation and heat movement. The plastic sheet was covered with an opaque cloth to prevent overheating of the chambers by solar radiation. The soil in

Table 1. Experiment dates, temperature ranges, and seed-piece fresh weights for thermogradient analysis.

Experiment	Date		Temperature Range	Seed Piece F.W.
	Start	End		
	Julian Day		° C	g
Dormancy Break				
5 days	42	47	20-30	40-60
10 days	37	47	15-30	40-60
Growth and Elongation				
12 days	51	63	12-29	50-60
7 days	56	63	13-26	50-60
9 days	67	76	12-18	50-60
Tuber Growth	112	122	8-24	80-90

the cups was watered at three day intervals. Temperatures of the water in the chambers and the soil next to the seed-piece of the central cup in each chamber were measured periodically. Seed-pieces having dormant buds were used to determine the temperature effect on dormancy break. Seed-pieces with already elongating buds were used to determine temperature effects on growth and elongation. After the thermogradient treatment the plants were washed, broken into components, measured, dried, and weighed.

To study the effect of temperature on tuber growth, 64 seed-pieces were planted in 25 cm plastic pots on 29 January (Julian day 29). The pots were arranged in an 8 by 8 pattern with border rows not utilized in experiments. Each pot was filled to 8 cm with sandy soil. The soil layer was covered with 4 mm mesh nylon net. According to Nosberger and Humphries (1965), this mesh is large enough to allow root penetration while small enough to keep tubers above the net. In this experiment, this method did not work as tubers were often found to grow below the net. One seed-piece per pot was placed directly on the net and covered with 15 cm of vermiculite.

The pots were watered regularly to prevent stress. On nights of predicted frost, all pots were covered with a 6 mil polyethylene sheet to prevent cold damage. On 28 February (Julian day 59) the seeds were checked. Fourteen pots were discarded due to seed-piece rot or continued dormancy. Eight pots had shoots near the vermiculite surface. These shoots were exposed to give more uniform emergence and equalize development with the remaining pots which had healthy emergent stems. Thus, on 28 February 100% emergence was obtained. Pots were fertilized on days 1 and 19 post-emergence. According to visual inspection of the

experimental and surrounding areas the plants were sprayed with Carbaryl and Captan to control Colorado potato beetle and late blight, respectively. Irrigation frequency was increased after 20 March due to higher temperatures and lower precipitation.

On day 19 post-emergence 58% of the pots had visible inflorescences. The ground cover was estimated at 95%. Tuber initials were formed on all of the ten border pots inspected. Therefore, 19 March (Julian day 78) was considered as the first day of flowering and the beginning of the linear growth phase. Twenty-two days after flowering, ten pots were placed in the thermogradient bath. The water was stabilized with four polystyrene baffles and ethyl malic anhydride (EMA-91). EMA-91, supplied by the Monsanto Corporation, forms a polymer which increased the viscosity of the bath to slow thermal transfer by convection both within and between the large chambers of this experiment. Two pots were placed in each of the five chambers formed by the baffles and the pots were protected from the EMA-91 by plastic bags. Five control pots were harvested before and five after thermogradient treatment. The control plots which were harvested after the treatment period were kept on the greenhouse bench adjacent to the thermogradient bath during the treatment period. All plants were separated into tubers, leaves, and remainder which included roots, stems, rhizomes, and inflorescences. The components were dried at 100° C and weighed.

RESULTS AND DISCUSSION

Growth Analysis 1978

Pre-Emergence

In the Julian day 33 planting, the seed-piece buds of both Monona (M33) and Sebago (S33) were still dormant. Bud dormancy break occurred after Julian day 45 for both cultivars as indicated by the stem length data in Figures 22 and 23. Bud break, the first major phenologic event of this planting date, required about two weeks. By the Julian day 73 planting the seed-piece buds of both Monona (M73) and Sebago (S73) had begun to elongate. Many of the elongating shoots were broken off during the planting operation. Significant stem growth did not begin again until after day 80, one week after planting (Figures 24 and 25).

Both M33 and S33 required about three weeks from the beginning of stem elongation until emergence. The average stem length at emergence was about 10 cm, the same as the planting depth. Therefore, these stems elongated at the rate of approximately 0.5 cm/day. The stems of M73 and S73 elongated nearly 0.7 cm/day, thus M73 and S73 only required two weeks from the beginning of stem elongation to emergence.

Root growth began within days after initial shoot elongation in all treatments. By the time of emergence the shoot to root ratios were 2.77 for M33, 2.69 for S33, 1.22 for M73, and 1.31 for S73.

The differences between planting dates can be attributed to the dormancy state of the seed-pieces at planting and edaphic factors. The edaphic factor of primary importance is temperature since soil nutrients and moisture were controlled by fertilization and irrigation, respectively. After bud dormancy break we may assume that the seed-pieces of both planting dates had similar physiologic status. Therefore, soil temperature will be the only major independent variable affecting stem and root growth until emergence. The average soil temperature from planting to emergence was 16° C for the Julian day 33 planting and 20° C for the Julian day 73 planting (Figure 10). This four degree temperature difference thus appears to be the main factor which increased the rate of shoot elongation and decreased the shoot to root ratio in the second planting date. The effect of temperature on time from planting to emergence is described by calculation of soil heat unit accumulation during this period. Using a base temperature of 9° C, both cultivars showed remarkable similarity in pre-emergence soil heat unit accumulation (Table 2).

Even though it seems safe to conclude that increased soil temperature speeds stem elongation and decreases the shoot to root ratio during the pre-emergence phenophase, the underlying physiological mechanisms are not clear. The soil temperature regulates the rate that the seed-piece makes substrate available to the growing organs. The soil temperature may also influence the rate at which the individual organs are capable of incorporating the available substrate. These two mechanisms represent the classical source strength versus sink strength controversy.

Table 2. Duration and cummulative heat units for Monona and Sebago phenophases.

Phenophase	Treatment (Cultivar and Planting Date)			
	Monona 33	Monona 73	Sebago 33	Sebago 73
Pre-Emergence				
Julian Days	33-66	73-94	33-68	73-15
Soil Heat Units*	225.8	225.7	238.1	239.2
Emergence to Flowering				
Julian Days	66-87	74-105	68-86	95-107
Air Heat Units**	117.7	108.3	107.2	112.1
Emergence to Tuber Initiation				
Julian Days	66-80	94-111	68-84	95-116
Soil Heat Units*	113.7	250.6	142.9	304.1
Air Heat Units	44.2	155.5	60.6	172.9

* Soil Heat Units = (°C-9); ** Air Heat Units = (°C-12.6)

Emergence

The date of emergence, as used here, is the date when the percent of seed-pieces with emergent stems reached half of its maximum value. The percentages of seed-pieces with emergent stems are graphed through time in Figures 14 and 15. The majority of M33 stems emerged during the 20 day period from day 60 to day 80. S33 stem emergence encompassed an even longer period, about 25 days, from day 60 to day 85. The M73 and S73 treatments emerged over a slightly shorter period, about 15 days. In any case, emergence was not at all uniform.

The final emergence percentage for Monona was significantly[1] greater than that for Sebago at both planting dates (Table 3). The poor emergence of Sebago resulted from disease of the seed-pieces. Furthermore, the emergence of the day 33 planting exceeded that of the day 73 planting. The low emergence of the second planting may have been due to improper storage conditions of the seed-pieces before planting or injury to the seed during the planting operation. Since the buds on the seed-pieces had already broken dormancy the seed-pieces may have been more susceptible to injury. Another possibility is that the seed rot became more widespread during the longer storage period of the seed used in the second planting. However, the primary factor responsible for the difference in emergence percentages between the two planting dates appeared to be soil surface temperature. Skies were clear and air temperatures high during the emergence period of the second planting. The surface layer of the soil dried and became very warm. On day 95 the soil temperature at 1 cm depth exceeded 30° C by

[1] Statistical analyses are presented in Appendix B.

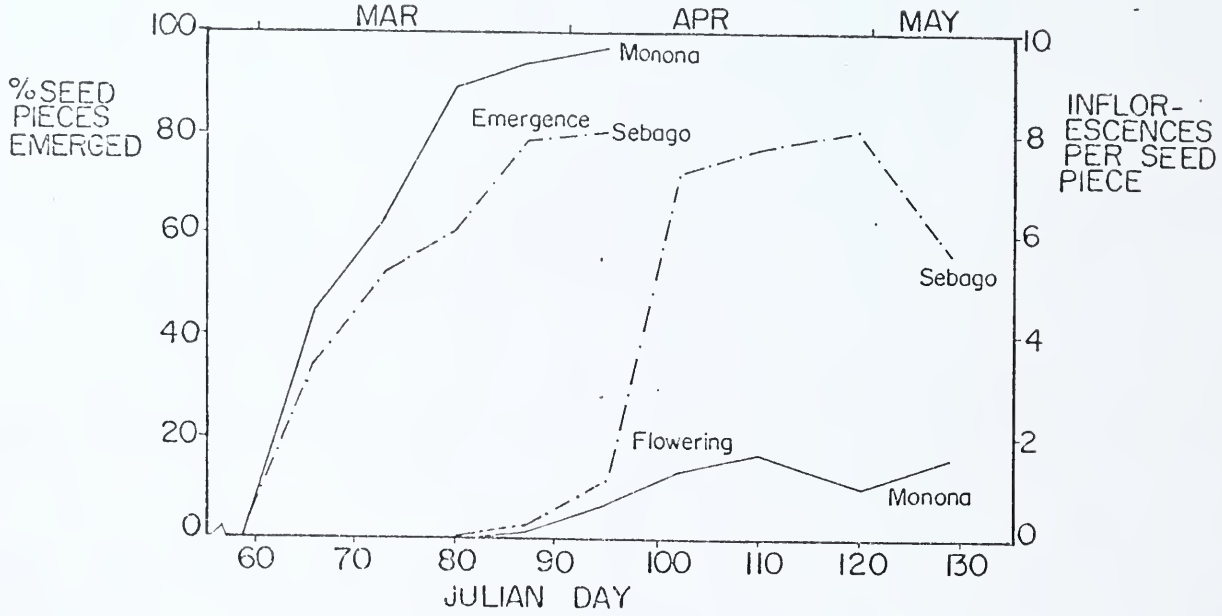

Figure 14. Percent seed-piece emergence and number of inflorescences per seed-piece for Monona and Sebago planted on Julian day 33.

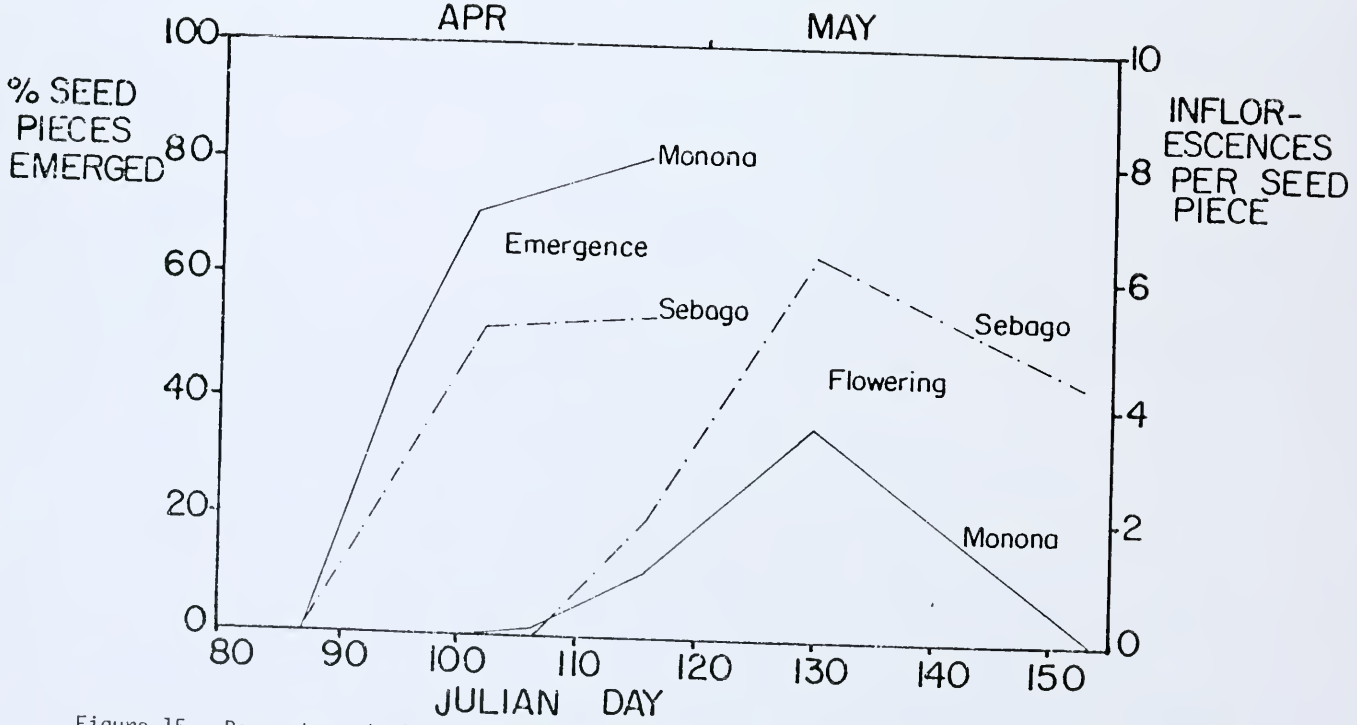

Figure 15. Percent seed-piece emergence and number of inflorescences per seed-piece for Monona and Sebago planted on Julian day 73.

Table 3. Seeding rates, maximum emergence, stems per seed-piece, and plant density for all treatments.

Treatment	Planting Rate	Final Emergence	Effective Seeding Rate	Stems Per Seed-Piece	Plant Density
	seed/m^2	%	seed/m^2		stems/m^2
Monona 33	4.30	98.4 ± 3.1	4.23	1.38	5.84
Sebago 33	4.30	76.5 ± 13.0	3.29	2.00	6.58
Monona 73	4.84	82.2 ± 5.38	3.98	2.00	7.96
Sebago 73	4.84	53.3 ± 4.88	2.61	2.44	6.29

1400 hrs. During the emergence period of the day 33 planting the temperature at 1 cm depth did not exceed 22° C on any day that the soil temperature profiles were measured. As will be shown below, a temperature of 30° C is high enough to inhibit shoot growth and will likely cause injury.

Plant Density

Though the planting densities were 4.3 seed/m^2 and 4.8 seed/m^2 for the day 33 and day 73 plantings, respectively, the wide range of final emergence percentage lead to effective seeding densities from 2.6 to 4.2 seed/m^2 (Table 3). As stated in the literature review, the seeding density is not the best measure of potato crop density. Rather, the main stem is taken to be the individual plant unit. Both cultivars compensated for low emergence by setting more stems per seed-piece. Sebago and Monona had significantly higher stems per seed in the day 73 planting than the day 33 planting. Sebago also had more stems per seed than Monona in both planting dates. The ultimate plant densities ranged from 5.8/m^2 to 7.8/m^2 with differences being insignificant.

Canopy Development

Leaf area and ground cover. After emergence aerial environmental factors begin to influence crop growth and development. Photosynthetically active radiation (PAR) provides energy for crop metabolic processes. The crop canopy intercepts PAR. Two parameters commonly used to describe crop canopies with respect to PAR interception are the leaf area index (LAI) and percent ground cover (GC). The LAI and GC for the four treatments are graphed in Figures 16 through 19.

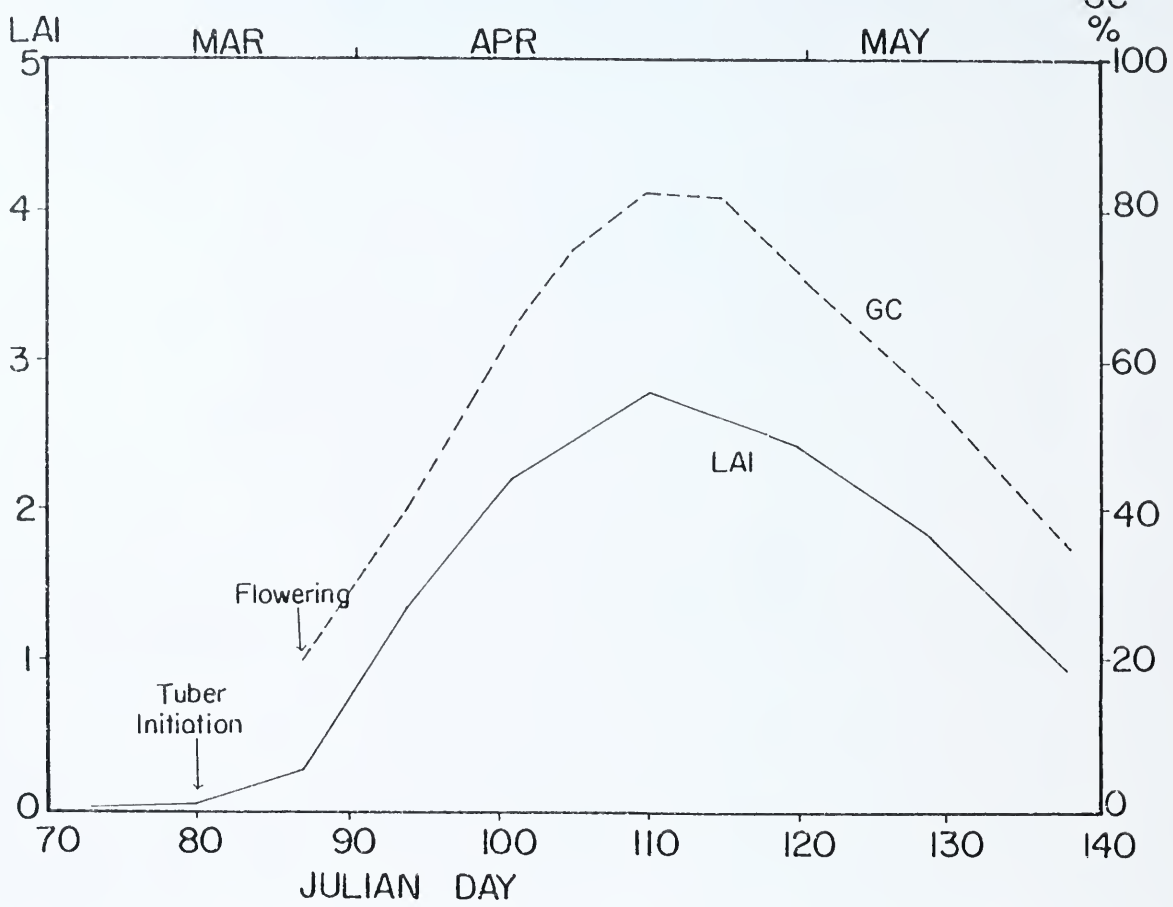

Figure 16. Leaf area index and percent ground cover for Monona planted on Julian day 33.

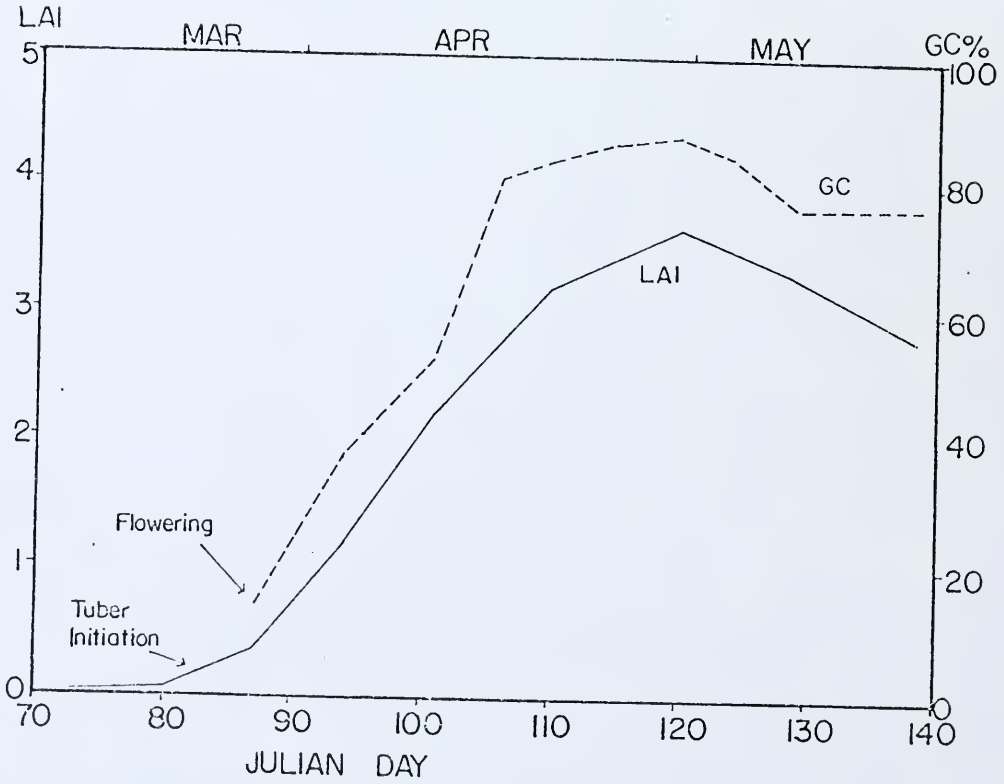

Figure 17. Leaf area index and percent ground cover for Sebago planted on Julian day 33.

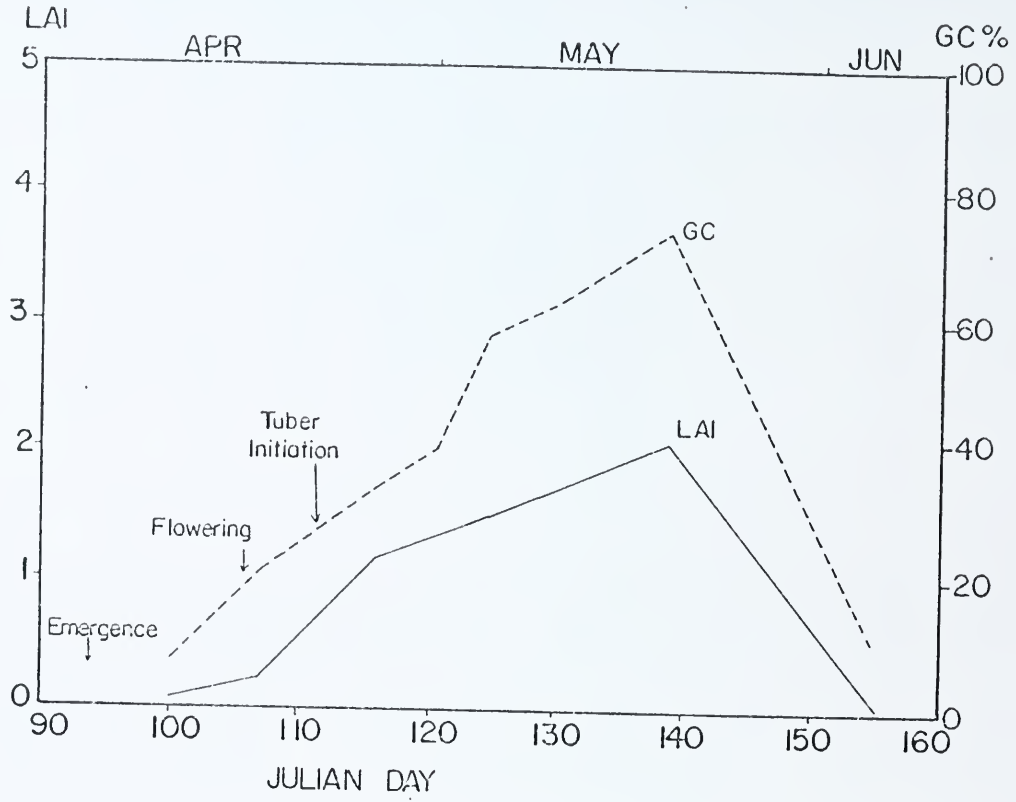

Figure 18. Leaf area index and percent ground cover for Monona planted on Julian day 73.

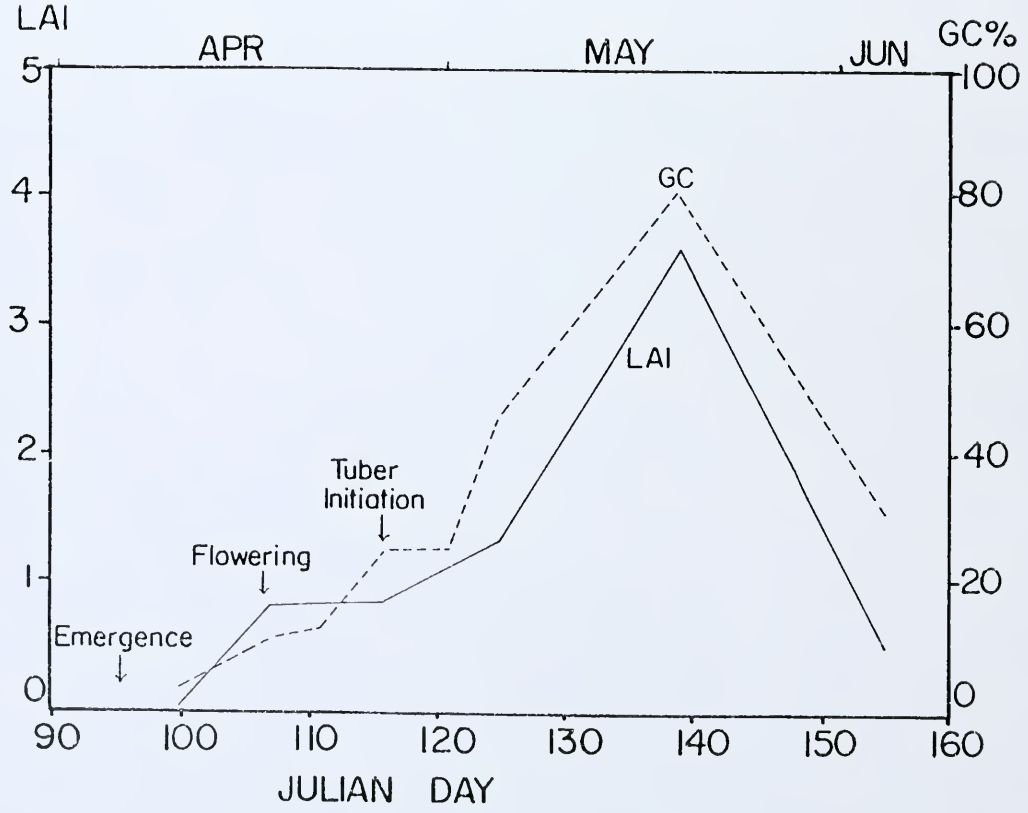

Figure 19. Leaf area index and percent ground cover for Monona planted on Julian day 73.

The curves for LAI and GC followed roughly parallel patterns for M33. The LAI increased to a maximum of about 2.7 at day 110. The GC also increased until day 110 when a maximum of about 80% was achieved. Both LAI and GC decreased gradually after their peaks at day 110.

The pattern was very much different for S33; however, S33 developed a larger canopy and maintained the canopy longer. The GC for S33 reached 80% by day 105 and maintained this GC through day 139. The LAI exceeded 3.0 by day 110 and peaked at about 3.6 on day 120. On day 139 the LAI of S33 was still almost 3.0 while that of M33 was below 1.0.

A greater canopy growth for Sebago was not evident in the second planting. Both S73 and M73 showed LAI and GC maxima at day 140 with fairly rapid canopy deterioration after this time. The maximum GC of S73 was about 81%, slightly greater than that of M73 at 76%. Although the peak LAI of S73 at 3.4 was much higher than that of M73, 2.0, since this is the only date which showed such a difference between LAI's of the two cultivars, the data point may be in error. Indeed, the leaf dry weights for M73 and S73 were similar at this time (Tables 6 and 7).

The rapid canopy decline after day 139 for both S73 and M73 was most likely due to high temperatures during this period. As shown in Figure 10, the air and soil temperatures increased steadily after day 110 with daily maxima exceeding 30° C by day 140. Thus, temperatures began to exceed the thermal maximum for potatoes about the same time as the beginning of canopy decline for the day 73 planting.

The differences between the Sebago and Monona canopies of the first planting date may be attributed to phenologic differences. By

exponential regression, M33 initiated tubers around day 80, whereas S33 initiated tubers some four or five days later. Initial tuber growth was also slower in S33 than M33 (Tables 4 and 5). The early initiation and growth of tubers in M33 likely reduced canopy development relative to S33. In other words, M33 partitioned a greater portion of its daily photosynthetic products into tuber growth than did S33.

As a tool for characterizing crop canopies with respect to PAR utilization, LAI is most useful after the crop canopy has closed. At full ground cover the LAI estimates the number of leaf layers light must penetrate before reaching the ground.

None of the crop canopies in this experiment reached full ground cover. In order to estimate the number of leaf layers the light can penetrate when entering the crop canopy, the LAI must be divided by GC. This parameter is termed the effective leaf area index (ELAI). The ELAI's for the treatments of this experiment are graphed in Figures 20 and 21.

M33 and S33 both reached an ELAI of 3.0 around day 93, 20 days before the maximum LAI and GC were achieved. For M33 the ELAI remained fairly constant near 3.2 from day 93 to day 120. The ELAI for S33 increased to about 4.0 by day 100 and plateaued at this level. Similarly, M73 and S73 reached an ELAI plateau around day 116, about 25 days before the peak of LAI and GC for these treatments. Though the LAI and GC were much greater in the first than the second planting, the same is not true for ELAI. These results indicate that both the Sebago and Monona canopies grow upward before they extend horizontally. The long period of constant ELAI suggests the GC alone can be used to estimate light interception during this time.

Table 4. Dry weights for various components of Monona planted on Julian Day 33, based upon samples of two seed-pieces per replicate.

Julian Day	Dry Weight								
	Seed-Piece	Stem	Root	Green Leaf	Chlorotic Leaf	Rhizome	Tubers	Inflorescence	Total
	- g/m^2 -								
66	54.14	1.4	0.5						56.1
73	30.0	1.2	1.0	0.8					35.3
80	29.4	2.4	1.1	4.4		0.1	0.1		37.4
88	18.9	6.6	2.4	19.2		0.5	0.4	0.01	48.0
95	21.2	19.4	4.4	73.1		1.6	19.5	0.49	139.7
102	11.6	32.6	4.7	103.5	3.3	1.9	71.5	1.68	230.9
110	13.0	41.1	3.5	101.3	4.0	1.8	116.7	1.94	283.4
120	8.6	45.4	3.5	98.2	15.2	1.8	363.8	1.32	549.8
129	6.7	53.8		60.9	31.6		527.9	0.96	681.9

Table 5. Dry weights for various components of Monona planted on Julian Day 73, based upon samples of two seed-pieces per replicate.

Julian Day	Dry Weight								
	Seed-Piece	Stem	Root	Green Leaf	Chlorotic Leaf	Rhizome	Tubers	Inflorescence	Total
	- g/m^2 -								
88	28.4	0.7	0.3						20.4
95	22.5	1.7	1.4	1.7					27.3
100	17.0	1.9	0.9	2.8					22.6
107	19.6	6.1	0.8	13.6		0.1		0.1	40.2
116	10.8	15.6	3.8	36.4	0.6	0.5	21.9	0.9	92.4
125	8.0	17.3	2.8	58.8	4.0	0.4	61.8	1.5	162.6
139	7.0	37.7	3.0	69.9	36.7	0.5	229.9	2.7	387.5
153	1.0	21.5	5.7	0.0	50.9	0.9	395.7		475.7

Table 6. Dry weights for various components of Sebago planted on Julian Day 33, based upon samples of two seed-pieces per replicate.

Julian Day	Dry Weight								
	Seed-Piece	Stem	Root	Green Leaf	Chlorotic Leaf	Rhizome	Tuber	Inflorescence	Total
	g/m^2								
66	46.7	1.0	0.4						48.0
73	22.8	1.1	0.9	0.3					25.1
80	19.0	2.0	1.5	2.9		0.1			25.5
88	10.6	5.7	2.4	11.6		0.5	0.4	0.1	31.2
95	6.9	22.5	5.2	55.7		1.7	5.0	1.2	97.9
102	5.7	43.0	4.7	83.7	3.2	1.8	33.3	2.9	178.3
110	2.8	68.6	3.8	102.1	5.1	1.6	68.4	6.9	259.4
120	4.2	111.6	5.6	118.6	20.7	2.4	240.6	13.7	517.4
129	0.7	70.2		55.6	19.4		314.8	3.9	464.5

Table 7. Dry weights for various components of Sebago planted on Julian Day 73, based upon samples of two seed-pieces per replicate.

Julian Day	Dry Weight								
	Seed-Piece	Stem	Root	Green Leaf	Chlorotic Leaf	Rhizome	Tubers	Inflorescence	Total
	- g/m^2 -								
88	32.2	0.2	0.1						32.5
95	19.3	0.1	0.5	0.1					20.6
100	17.8	1.0	0.8	0.6					20.1
107	16.5	2.6	1.4	4.1				0.1	25.4
116	2.6	10.3	2.8	33.0	0.4	0.3	0.9	0.8	51.0
125	4.3	25.8	3.8	65.3	5.0	0.5	16.7	3.2	124.6
139	0.9	108.4	3.1	55.0	42.2	0.5	96.2	8.9	315.0
153		112.2	3.5	18.5	103.0	0.1	249.1	19.8	516.4

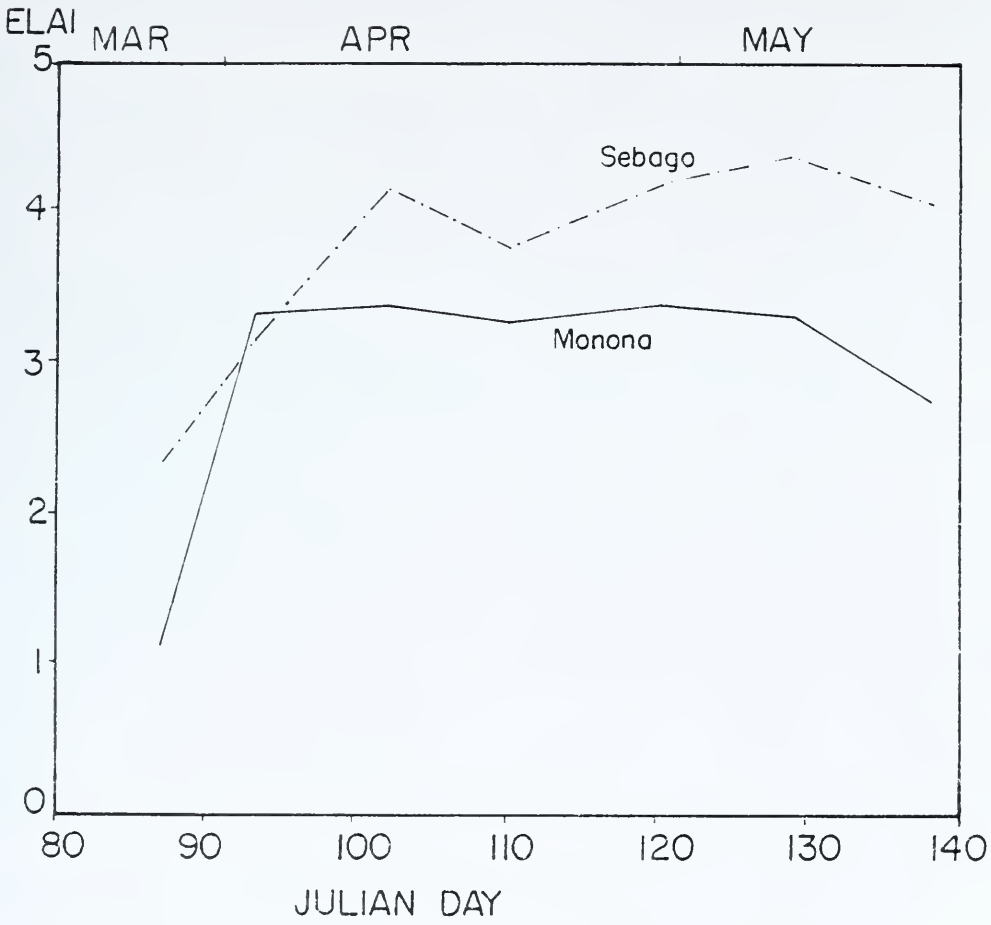

Figure 20. Effective leaf area index for Monona and Sebago planted on Julian day 33. ELAI = LAI/GC.

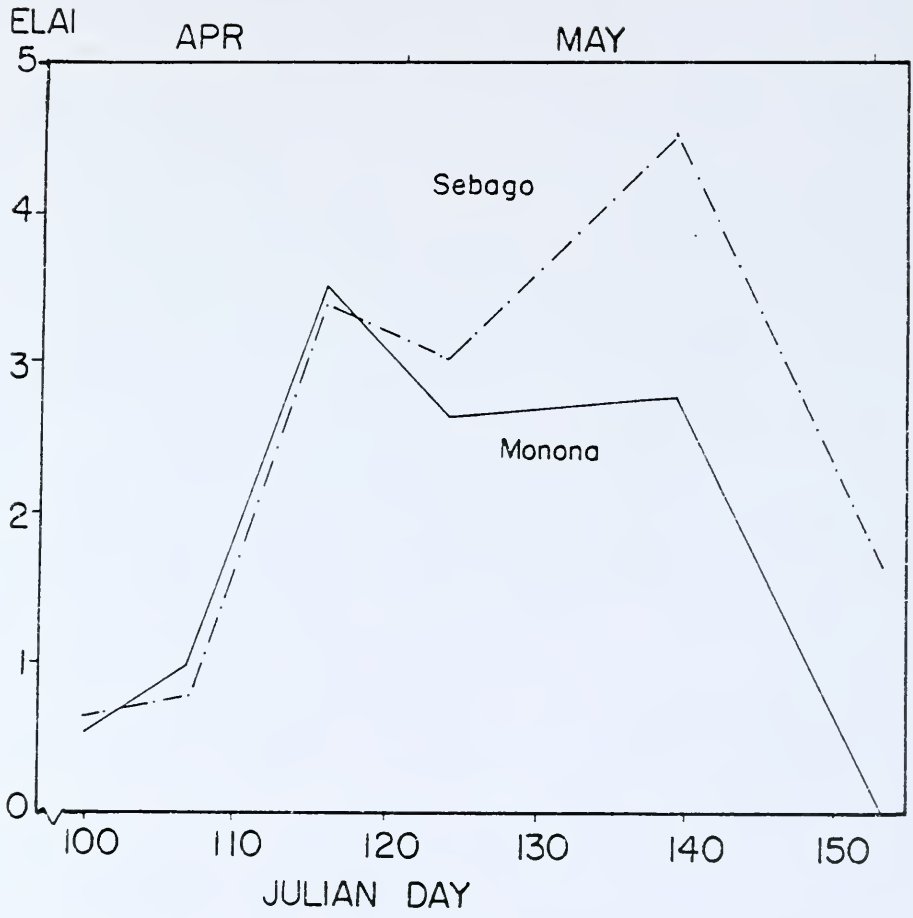

Figure 21. Effective leaf area index for Monono and Sebago planted on Julian day 73. ELAI = LAI/GC.

In potato canopies, as with most crops, the incident PAR is almost completely intercepted if the ELAI is 3.0 or greater. Apparently, after passing through three layers of leaf the light intensity is very near the light compensation point (Radley, 1963). The canopy growth morphology was similar for all treatments of this experiment. The canopy grew upward until the light intercepted was fully utilized, when the ELAI reached 3.0. Then the canopy grew outward, maintaining the ELAI at a level where PAR was fully intercepted.

One may question the efficiency of such a canopy. Higher photosynthetic rates may result from more rapidly increasing GC than ELAI. However, potatoes do require intense husbandry. Late blight and Colorado potato beetle do require repeated pesticide applications. Long stems would get killed by tractor wheels. Thus, high GC and long stems would be disadvantageous in this cultivation system.

Stem elongation. The LAI and GC characterize the photosynthetic system of the crop canopy. They do not, however, give much information about the structural support of the photosynthetic surfaces. The average main stem length, average branch length, and total branch and stem length per square meter can be used to characterize the structural support system (Figures 22 through 25).

The main stems of M33 and S33 lengthened until about day 100 with a maximum main stem length of about 62 cm for S33 and 54 cm for M33. Since the main stems terminated in inflorescences it is not surprising that main stem elongation ceased soon after floral initiation. Floral initiation is marked on the graphs at the point when inflorescences were first visible. The point of maximum main stem length coincided exactly with the time of peak flowering (Figure 14), as one would expect.

For M73 and S73, however, the time of maximum main stem length and maximum flowering did not coincide. For both cultivars the average main stem reached its greatest value, about 32 cm, by day 116 (Figures 24 and 25). The maximum flowering was not reached until day 129 (Figure 15). Since the number of inflorescences per seed-piece was greater than 1.0 for both S73 and M73 at day 116, it is likely that the majority of the main stems would have incipient if not visible flowers at this time. The further increase in flowering, then, might represent either incipient main stem inflorescences or florescing branch termini.

The average branch length was significantly greater for S33 than M33 on all days observed. The total stem plus branch length of S33 was significantly greater than that of M33 after day 100. This result is consistent with the findings of greater LAI, GC, and ELAI in S33 as compared to M33. On the other hand, differences between the total, main stem, and branch length for S73 and M73 were not significant.

The effect of planting date on stem and branch growth was marked. The stems and branches of the day 73 planting were much shorter than those of the day 33 planting. The difference in branch and stem length between the two planting dates is consistent with the results of LAI and GC measurements. Stem and branch growth is stopped by flowering. The earlier termination of stem and branch growth in the second planting was probably due to the warmer temperatures which hastened flower initiation. Flowering appeared to be regulated by heat (Table 3). With warmer temperatures in the second planting flowering was hastened, as was the completion of stem and branch elongation.

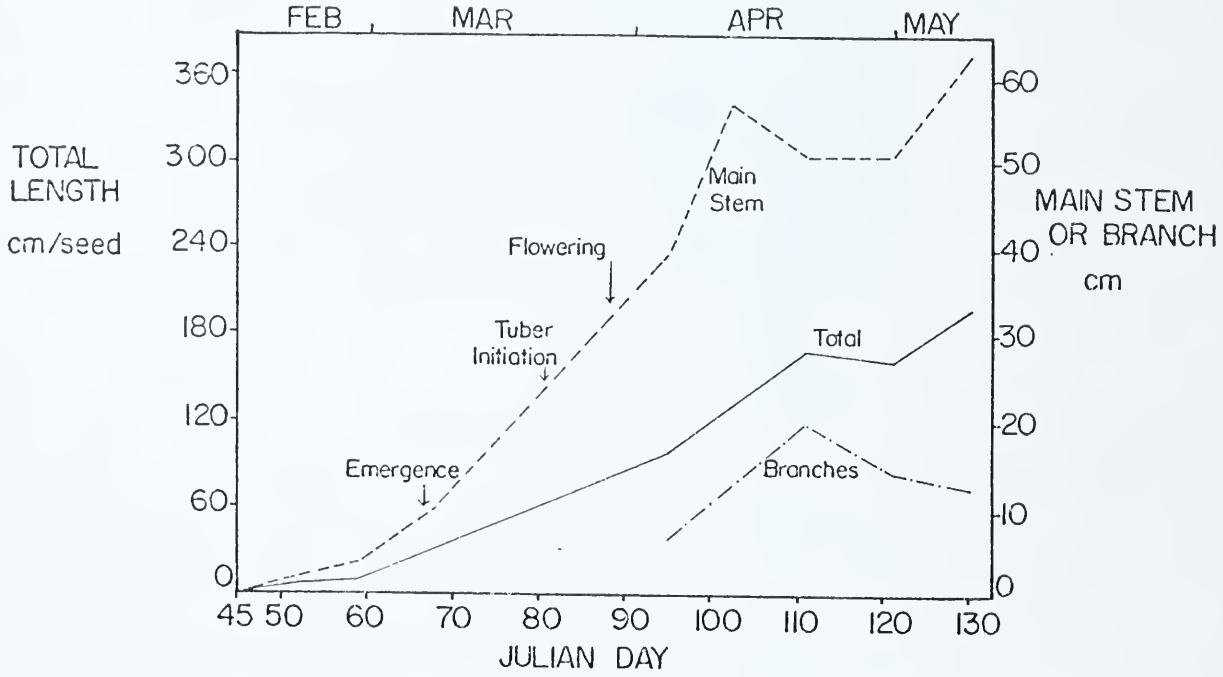

Figure 22. Total stem and branch length, main stem length, and average branch length for Monona planted on Julian day 33.

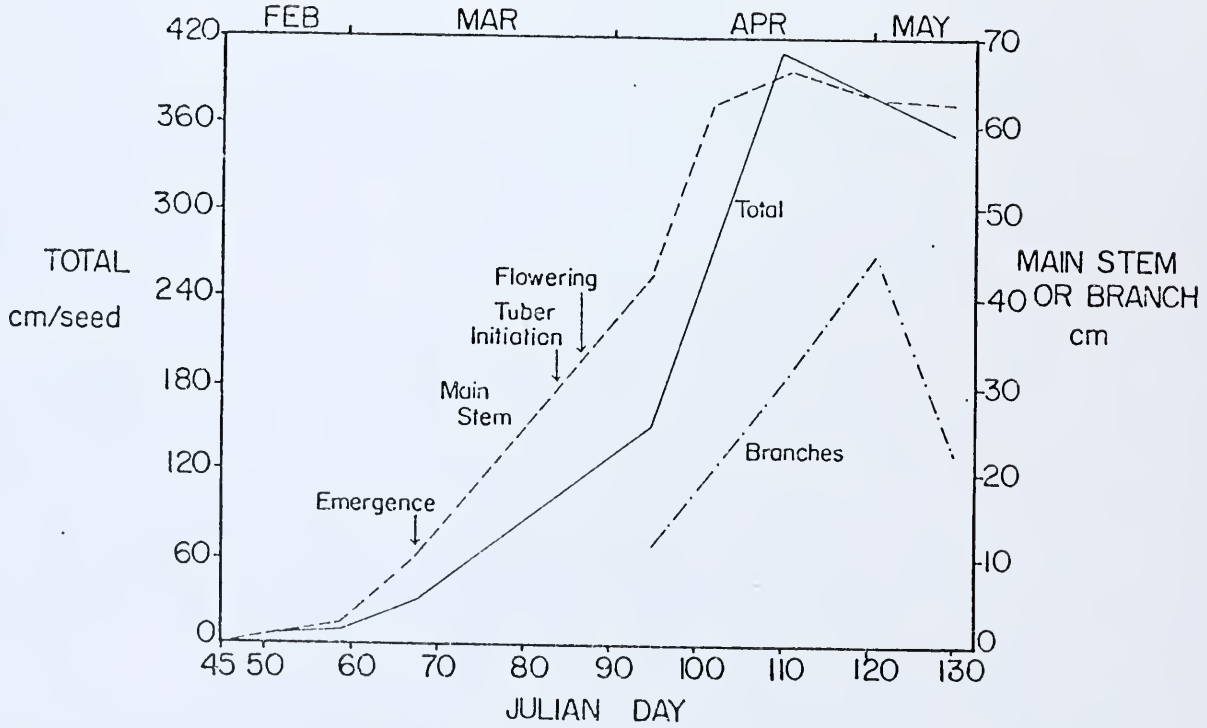

Figure 23. Total stem and branch length per seed piece, main stem length, and average branch length for Sebago planted on Julian day 33.

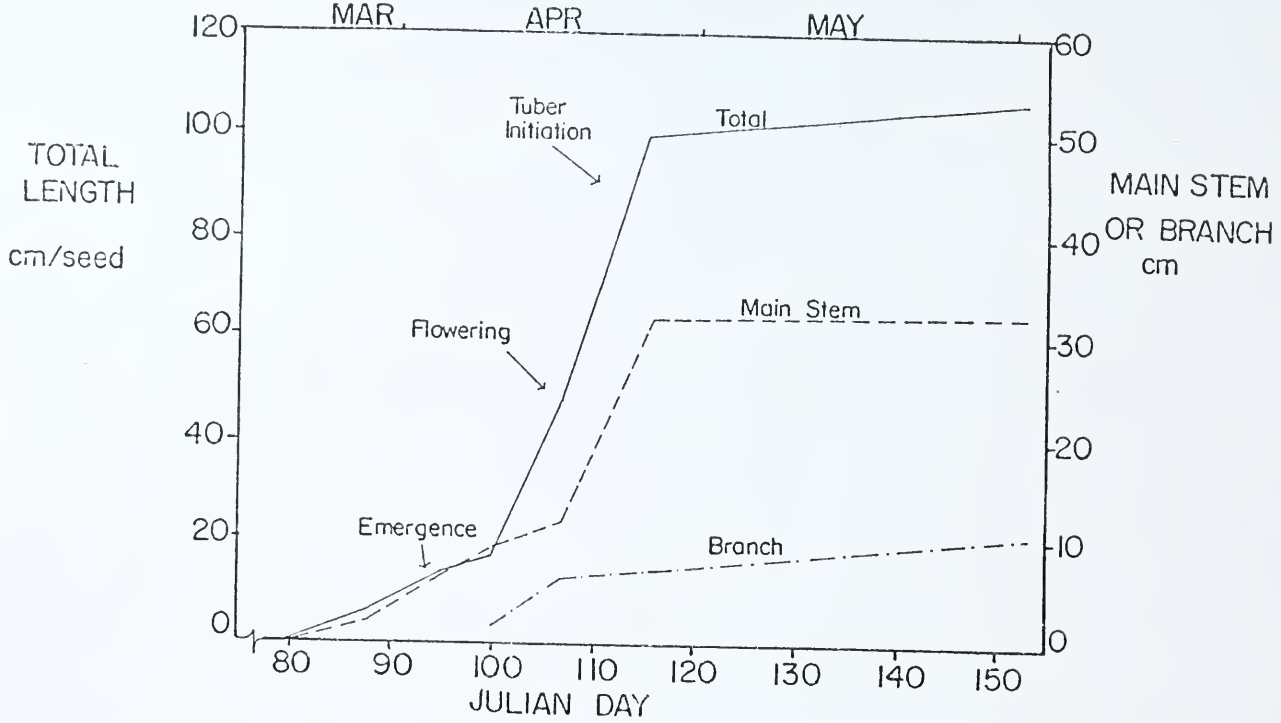

Figure 24. Total stem and branch length per seed piece, main stem length, and average branch length for Monona planted on Julian day 73.

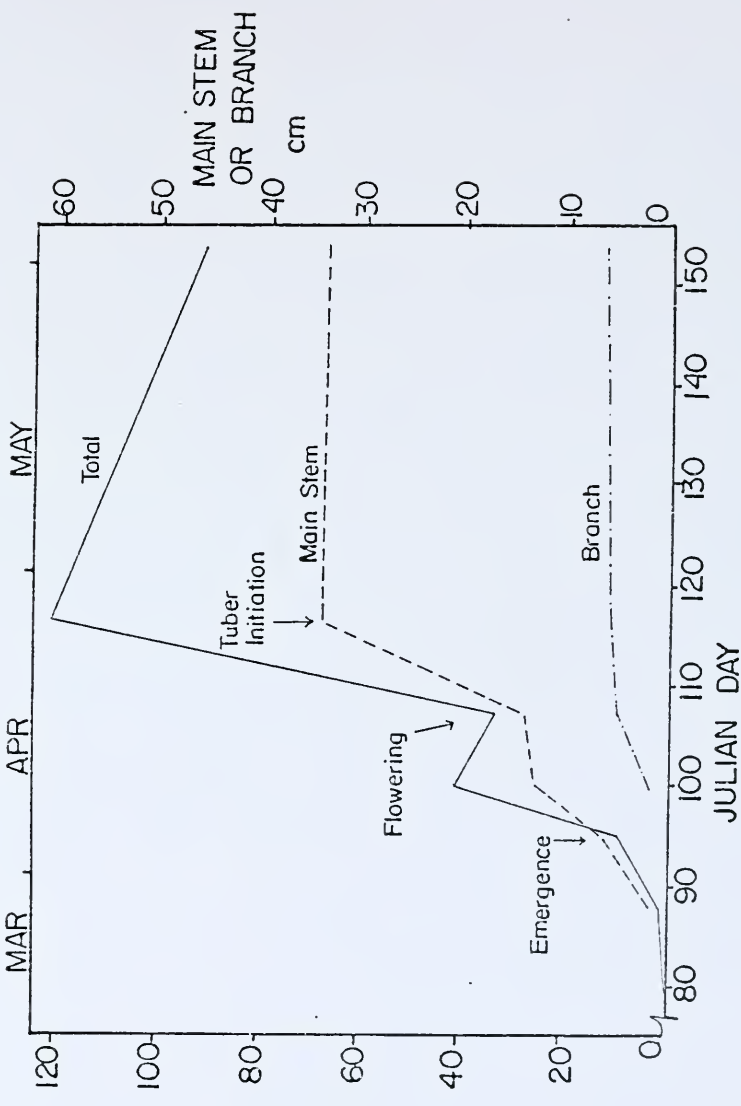

Figure 25. Total stem and branch length per seed piece, main stem length, and average branch length for Sebago planted on Julian day 73.

Canopy senescence. Maturity of annual crops is accompanied by senescence of the crop canopy. Decline of potato canopies in the Hastings area is generally due to high temperatures late in the growing season. As noted above, the canopy decline of M73 and S73 after day 139 can be attributed to excessive temperatures. A parameter which can be used to characterize canopy senescence is leaf duration. The leaf duration is the length of time a leaf remains physiologically active in photosynthesis. Leaf senescence includes chlorophyll degeneration and chlorosis. One method of estimating leaf duration is to determine the temporal difference between the dry weight curves for green and yellow leaves as in Figures 26 through 29. This method assumes that the oldest leaves senesce first. There are two main sources of error in this method of estimating leaf duration. First, it is difficult to recover all senescent leaves, especially later in the season after the senesced leaves have begun to abscise. This source of error may be minimized by placing greater importance on early observations of chlorotic leaves. Second, leaf duration estimations will err if the specific leaf weight (SLW) of the chlorotic and green leaves are greatly different. If a large portion of the leaf nutrients and assimilates are mobilized and translocated to other crop organs, then this method overestimates leaf duration. There was indeed a significant drop in SLW of green leaves as the canopy aged (data not reported). The decline in green leaf SLW with age can be explained by both leaf expansion and translocation effects. More importantly, since the SLW drops long before leaf abscission the difference between SLW of green and chlorotic leaves is lessened.

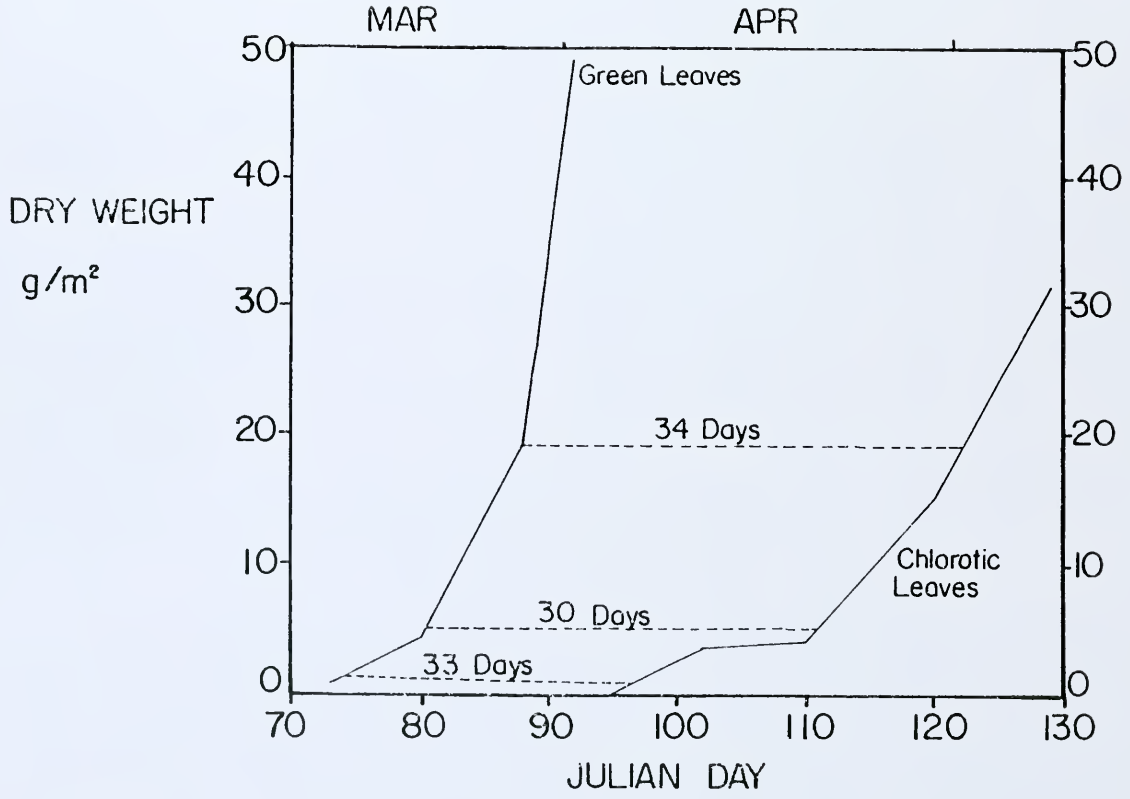

Figure 26. Dry weights of green and chlorotic leaves of Monona planted on Julian day 33 as used to estimate leaf duration.

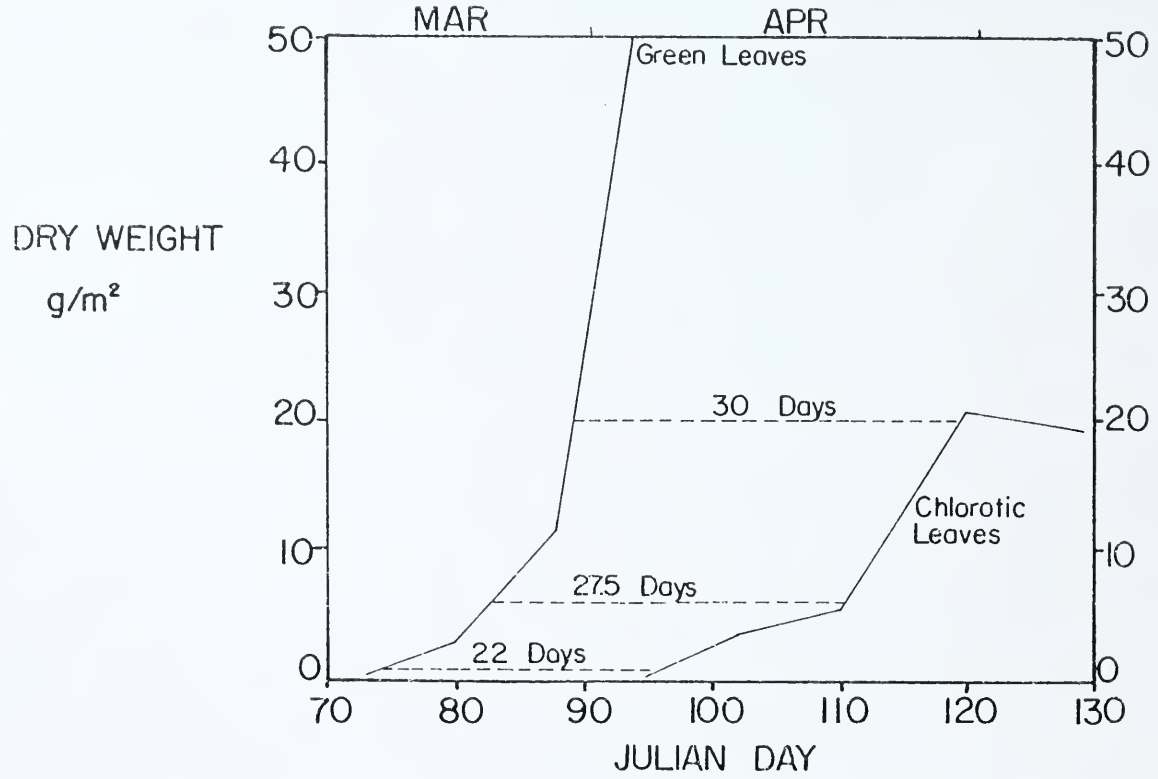

Figure 27. Dry weights of green and chlorotic leaves of Sebago planted on Julian day 33 as used to estimate leaf duration.

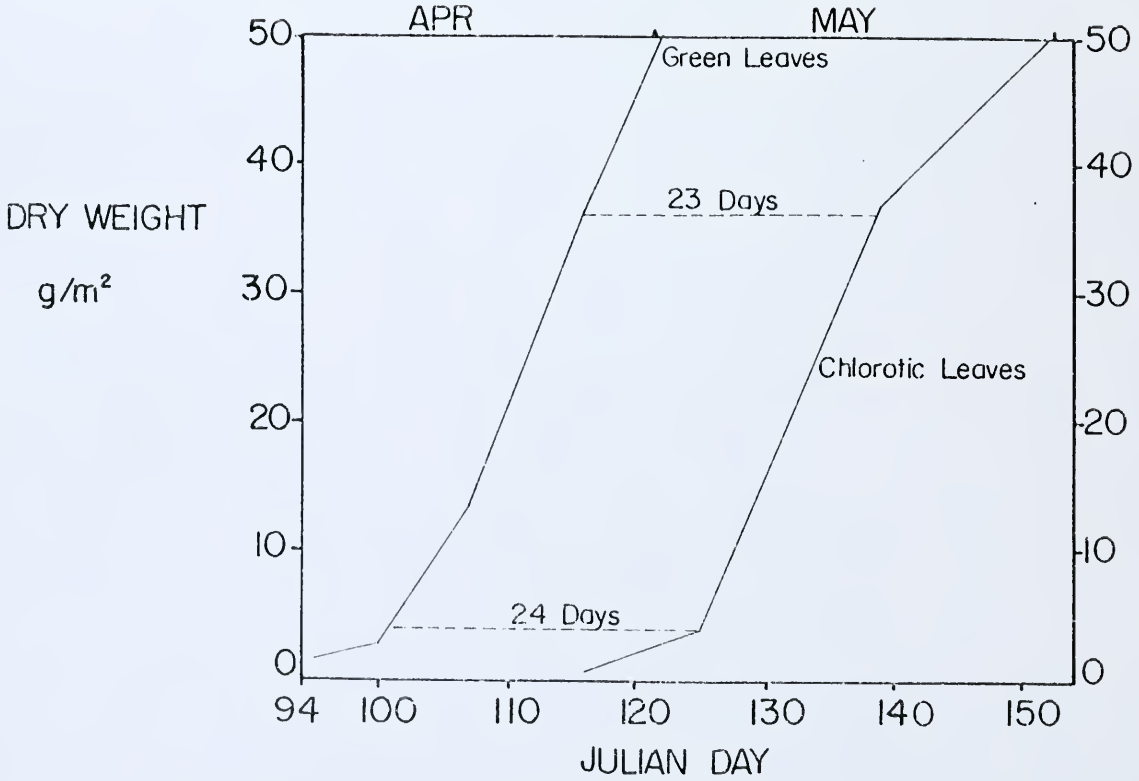

Figure 28. Dry weights of green and chlorotic leaves of Monona planted on Julian day 73 as used to estimate leaf duration.

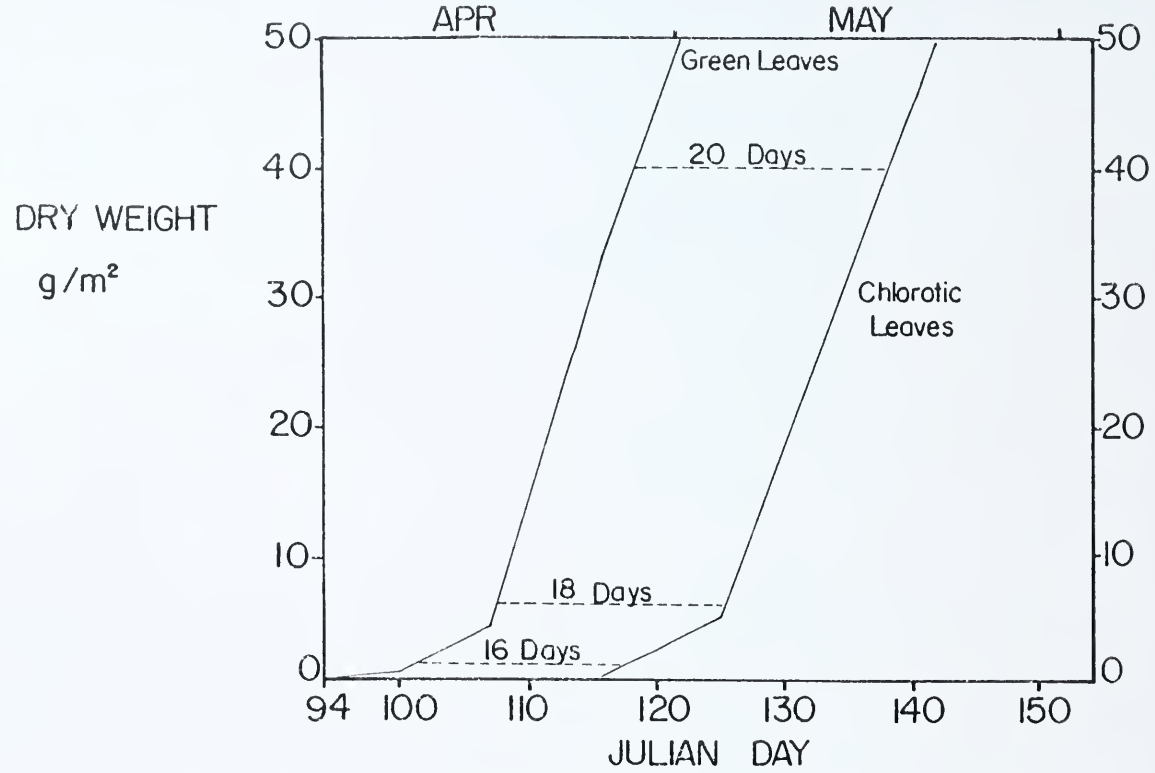

Figure 29. Dry weights of green and chlorotic leaves of Sebago planted on Julian day 73 as used to estimate leaf duration.

Two significant differences can be observed in this leaf duration data. The leaf duration of Monona is longer than that of Sebago, and the leaf duration of the day 33 planting was longer than that of the day 73 planting. The effect of planting date can be related to both environmental and physiological processes. The higher temperatures of the second planting sped leaf development and, when temperatures became excessive, injured the leaves through heat damage. More rapid development and heat injury will both hasten chlorosis.

Flowering

The next heat regulated phenophase after emergence is florescence (Table 3). The numbers of inflorescences per square meter are graphed in Figures 14 and 15. Sebago and Monona initiated flowers at about the same time for a given planting date. There were no significant differences between the peak numbers of inflorescences of the two plantings. Sebago, however, produced more inflorescences than did Monona. Furthermore, Sebago matured many fruits while Monona did not. The dry weights of these fruits are included in the inflorescence columns of Tables 4 through 7. As the inflorescence numbers, the dry weights of the flowers and fruits showed that Sebago produced heavier inflorescences than Monona while there was no significant effect of planting date.

Tuber Initiation

Heat unit accumulation predicts the phenophase durations from planting to emergence and from emergence to flowering (Table 3). The mean daily soil and air temperatures are used to predict emergence and floral initiation, respectively. On the other hand, neither soil nor air heat accumulation predicts tuber initiation. Indeed, no reasonable

base temperature can be derived to predict tuber initiation. Only a base temperature greater than ambient temperatures can be used to equalize heat unit accumulation between the two plantings. Using such a base, though mathematically feasible, does not make physiological sense, since such accumulated units would have negative values. A possible explanation for these tuber initiation results is the temperature versus carbohydrate availability mechanism described in the literature review. Presumably, cooler temperatures inhibit canopy growth but not photosynthesis. If canopy growth does not utilize the photosynthate of a given day, then the available carbohydrate level on the plant is high and may either stimulate tuber initiation or reduce photosynthesis by feedback inhibition.

Rhizomes

Just as one must analyze the stems and branches when interpreting the development of the crop's photosynthetic system, one must consider the tuber support system to fully understand tuber growth and functioning. Rhizomes are rather small, horizontally growing underground stems. Both M33 and S33 initiated rhizome development around day 80, barely ten days after emergence. The rhizome dry weight increased to a plateau near day 95 (Tables 4 and 5). M73 and S73 were slower to initiate rhizomes. In other words, rhizome initiation and tuber initiation had similar patterns with rhizome development slightly offset to precede tuber initiation. Presumably, rhizome and tuber development are regulated by the same mechanism since one grows from the other. Yet, if tuber initiation is stimulated by high labile carbohydrate levels in the plant associated with high photosynthesis rates and low canopy growth rates at the linear phase of total crop growth, then

rhizome development requires another explanation. Rhizomes initiate before tubers. Rhizomes in this experiment initiated before the linear crop growth period. They began development when the canopy appeared to be still utilizing seed-piece substrates for growth. The present data are not sufficient to explain these phenomena, they merely pose the question.

Yield Dynamics

The large carbohydrate reservoir in the potato's vegetative propagule may give potatoes an advantage in early canopy growth over crops with smaller propagules. The results of these experiments, however, indicate otherwise. The total crop weight did not increase significantly until 30 or more days after emergence in M33 and S33 (Figures 30 and 31). Although the canopy grew during this period, the canopy grew by translocation from the seed-piece rather than from canopy photosynthesis. Just as a leguminous crop will utilize soil nitrogen supplied before fixing atmospheric nitrogen, potato canopies deplete the seed-piece substrate before they begin auto trophic growth. Once positive growth did begin, presumably when the seed-piece carbohydrate reservoir was inadequate to meet the growth needs of the canopy, crop growth for all treatments is approximately linear and remained so until final harvest.

Crop growth in the day 73 planting was similar to that in the day 33 planting (Figures 32 and 33). The crop growth rate was zero for the first 20 days after emergence and became linear soon thereafter. The common pattern for crop growth is an exponential growth phase, or lag phase, which leads into a linear growth phase after the maximum ground cover is reached. The large vegetative propagule of the

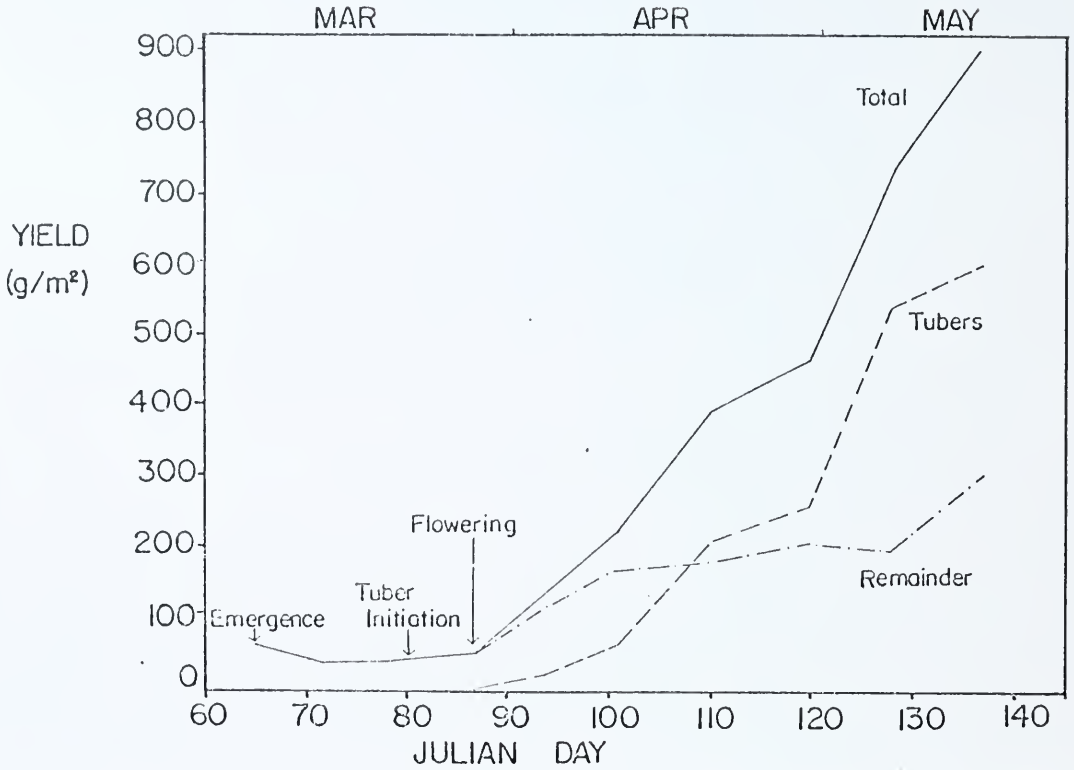

Figure 30. Growth curves for total plant, tubers and remainder for Monona planted on Julian day 33 with sample size from 12 to 20 seed-pieces per replicate.

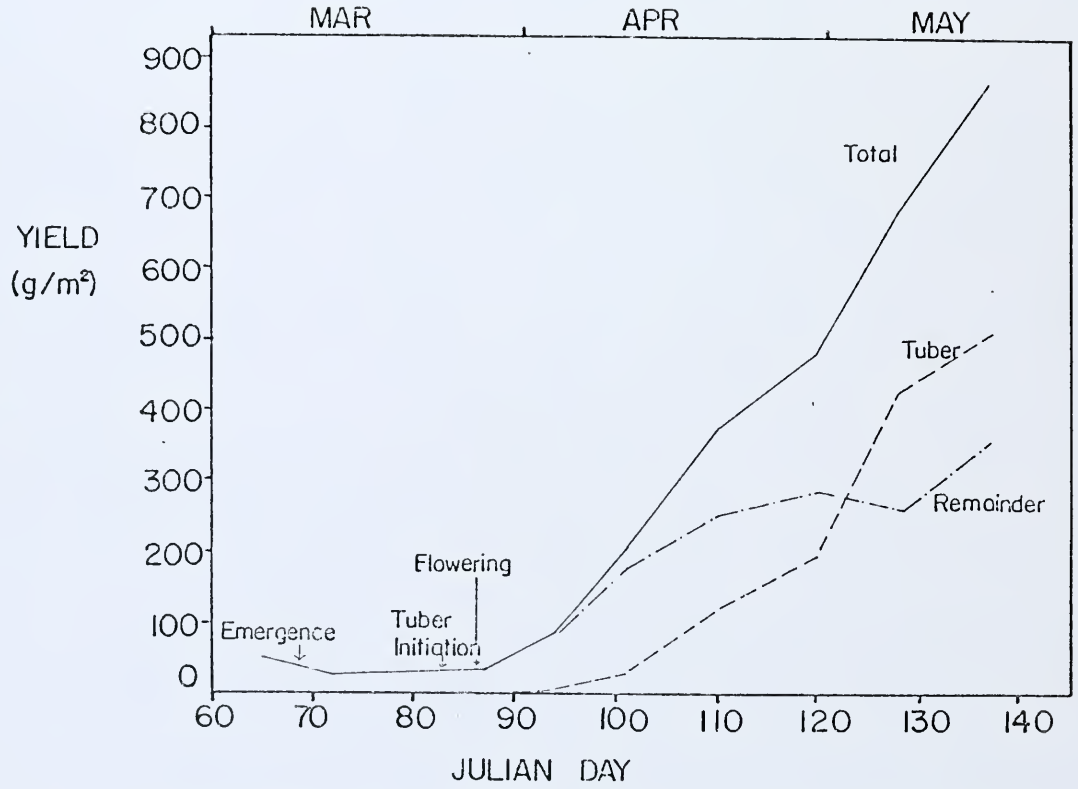

Figure 31. Growth curves for total plant, tubers, and remainder for Sebago planted on Julian day 33 with sample size from 12 to 20 seed-pieces per replicate.

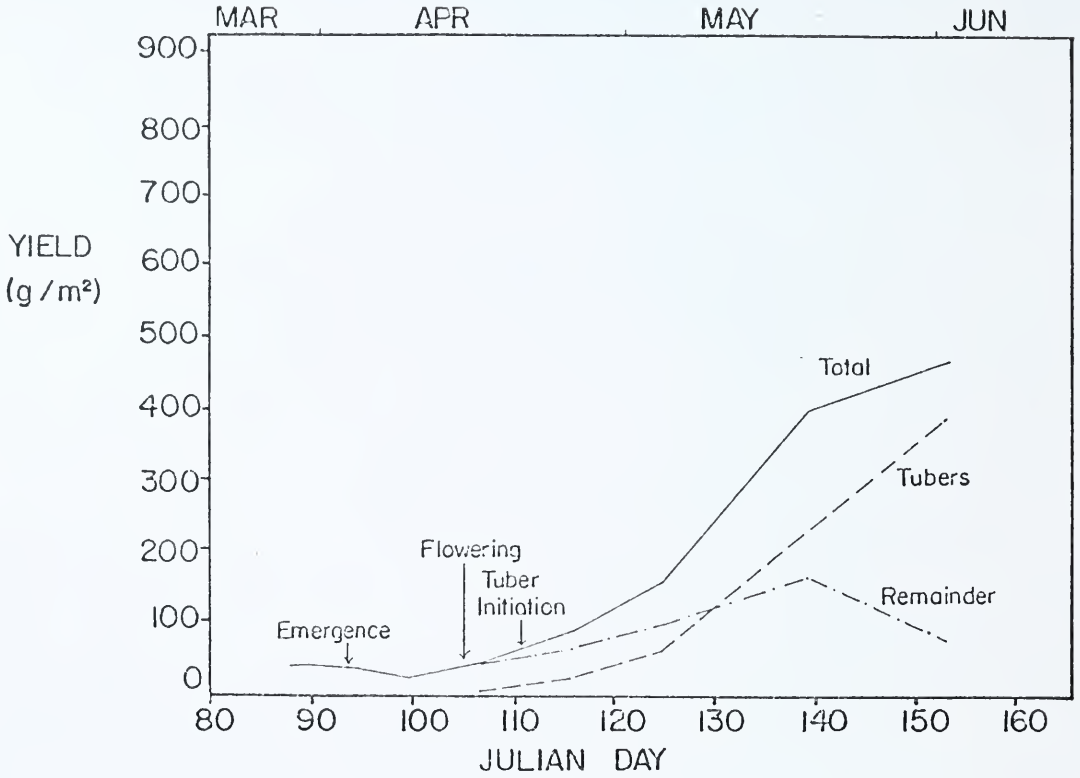

Figure 32. Growth curves for total plant, tubers, and remainder for Monona planted on Julian day 73 with sample size from 12 to 20 seed-pieces per replicate.

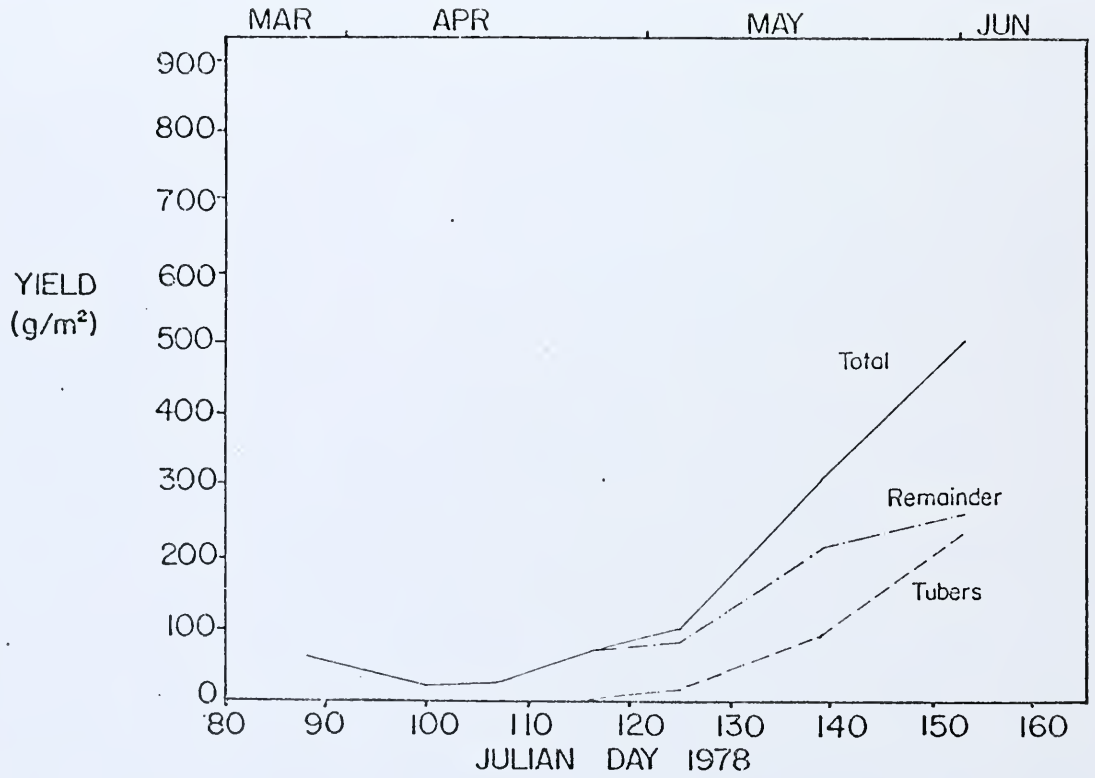

Figure 33. Growth curves for total plant, tubers, and remainder for Sebago planted on Julian day 73 with sample size from 12 to 20 seed-pieces per replicate.

potato reduces or eliminates the exponential phase. Unfortunately, the long zero growth phase of the potato crop during initial canopy growth has the same net result as an equally long lag phase for a crop propagated by units with smaller substrate reservoirs.

In all treatments, tuber initiation occurred at about the same time as commencement of linear growth. If high labile carbohydrate pool levels stimulate tuber initiation, as suggested above, it is logical that tuber initiation should closely follow the onset of autotrophic growth. The crop and tuber growth rates with their respective periods of estimation are given in Table 8. All linear models are significant as indicated by the high r^2 values. Both the crop and tuber growth rates were faster in the day 33 than the day 73 plantings. This difference between the growth rates of the two plantings is likely related to differences in ultimate canopy size. The day 33 planting achieved higher ground cover percentages and LAI's than the day 73 planting. The maximum growth rate for most crops is from 20 to 22 $g/m^2/day$. The crop growth rates in all treatments of this experiment were significantly below this rate. However, when the low crop growth rates of M33 and S33 are divided by their respective maximum ground covers, the results are both around 21.5 $g/m^2/day$. Although the growth rates were not significantly different between cultivars, the tuber growth rate was slightly higher for Monona than Sebago. Furthermore, both the crop and tuber growth rates became linear sooner in Monona than Sebago.

The tuber growth rate showed a short lag phase, about one week, for all treatments. The combination of no exponential crop growth phase and a short exponential phase for tuber growth not only simplifies

partitioning analysis, but also makes such analysis more meaningful since it compares simultaneous growth rates. The percentage of daily photosynthate partitioned to tuber growth can be estimated by the ratio of tuber and crop growth rates (Table 8). Partitioning to tubers was greater in the first than the second planting and slightly higher for Monona than Sebago as one would expect from the tuber growth rates.

The Monona cultivar outyielded Sebago in tubers for both plantings. The total biomass yield did not differ between the cultivars. The higher tuber yields of Monona can be attributed to two factors: 1) Monona reached the linear tuber growth phase sooner than Sebago, thus it had a longer filling or bulking period; 2) Monona partitioned a greater portion of its daily photosynthetic products into tuber growth.

Thermogradient Analysis 1979

Bud Dormancy

The length of tuber bud dormancy is influenced by several factors including length of storage, wounding, moisture, nutritional level of the crop which produced the seed-pieces, and the soil temperature. The only factor of interest here is soil temperature. Figures 34 and 35 show the growth and elongation of buds which were dormant at sowing. According to both growth and elongation results, soil temperatures from 18 to 24° C are optimum for dormancy break. No buds had broken dormancy after five days at 27° C or after ten days at 29° C. Although temperatures below 15° C were not tested, the degree of dormancy break after ten days at 15° C was less than dormancy break at warmer temperatures.

Table 8. Crop and tuber growth rates during most linear growth period, with statistics for linear model and partitioning ratio.

Calculation	Monona 33	Sebago 33	Monona 73	Sebago 73
Crop Growth Rate ± s.e.	17.0 ± 0.528	16.5 ± 0.629	13.8 ± 0.759	12.4 ± 0.953
r^2	0.9747	0.9624	0.9679	0.9189
s.e.(linear model)	48.4	57.7	24.9	53.5
n	28	28	12	16
Period (Julian Day)	88-138	88-138	116-139	116-153
Tuber Growth Rate ± s.e.	14.3 ± 0.590	13.5 ± 0.811	9.05 ± 0.379	6.90 ± 0.685
r^2	0.9624	0.9386	0.9744	0.9021
s.e. (linear model)	44.3	45.2	21.3	27.1
n	24	19	16	12
Period (Julian Day)	95-138	102-138	116-153	125-153
Partitioning Ratio TGR/CGR	0.841	0.818	0.656	0.556

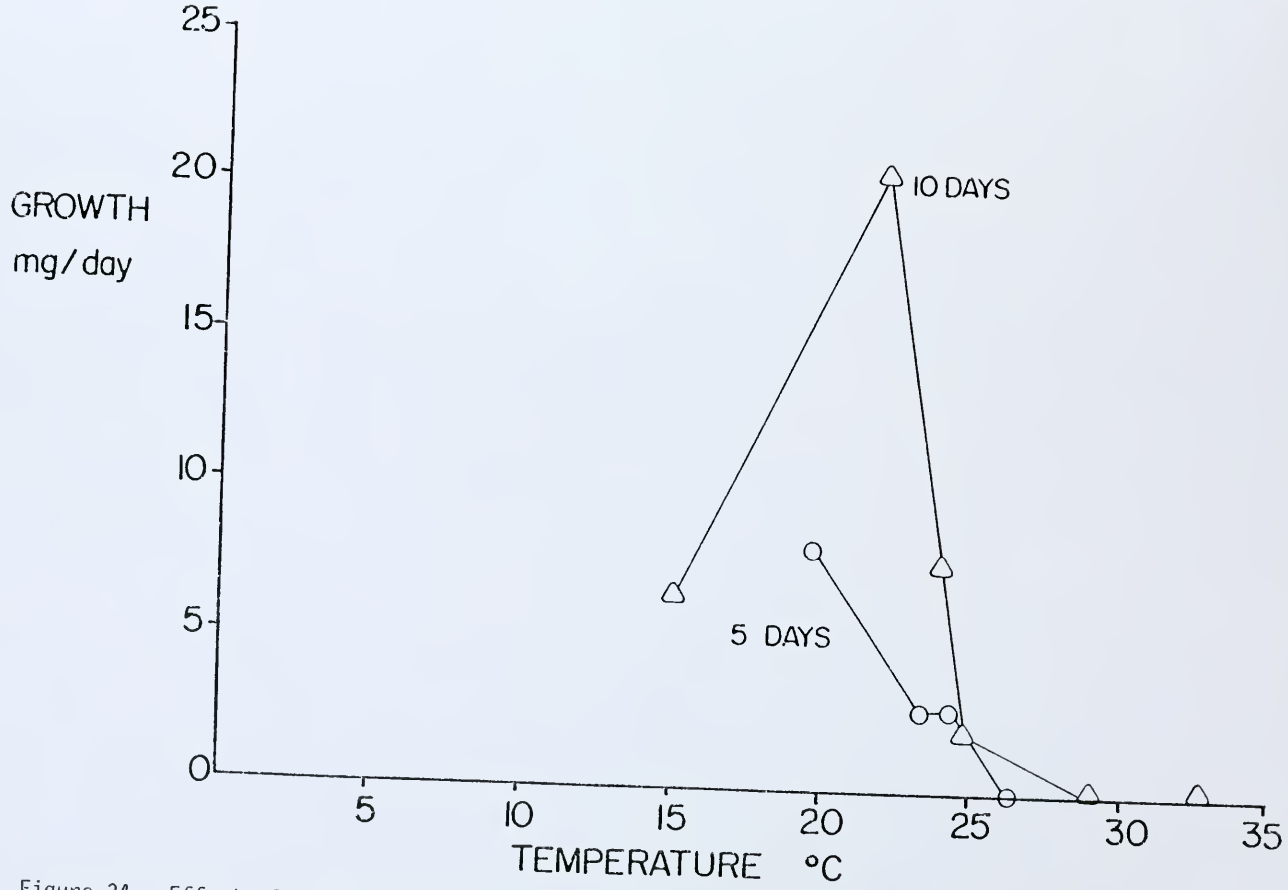

Figure 34. Effect of temperature on stem growth for Sebago seed-pieces with dominant buds. Growth measured after 5 (○) or 10 (△) days.

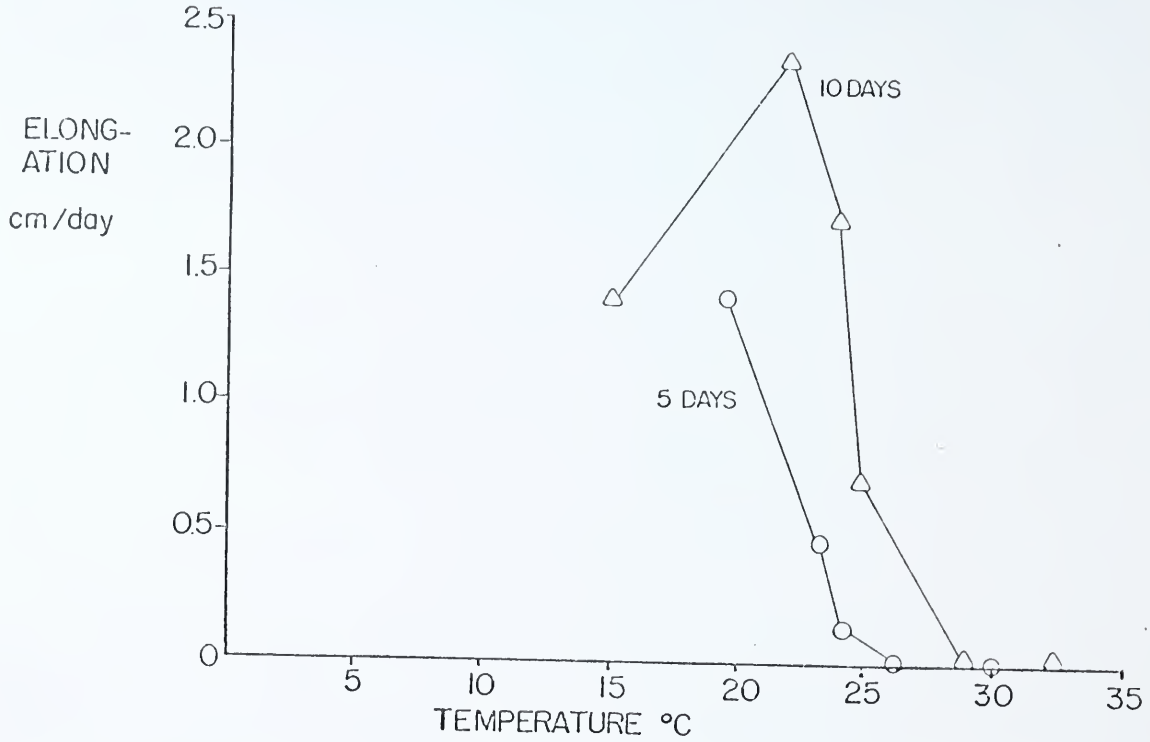

Figure 35. Temperature response for stem elongation in Sebago seed-pieces with dormant buds. Measured after 5 (O) and 10 (Δ) days.

Both the growth and elongation rates used here assume a linear growth model. Since the buds were dormant at planting, estimating daily growth with a linear model will necessarily err. However, the error appears slight since the range of growth and elongation rates estimated by the linear model correspond well with the growth and elongation rates of buds which had already begun growth at sowing (Figures 36 and 37). Another possibility is that neither dormant nor elongating buds have linear growth rates.

Stem Growth and Elongation

The potato seed-piece stores an enormous substrate supply for a newly initiated stem or root. Thus one may assume that the substrate supply from the tuber to the stem will be as great as the shoot initial can utilize. In other words, substrate supply will not limit initial shoot or root growth.

Soil temperature markedly influenced the growth and elongation of young stems (Figures 36 and 37). The optimum temperatures for stem growth ranged from 20 to 22° C. The rate of stem growth increased with the experiment duration. This growth rate increase was fitted to an exponential model whose coefficient is the relative growth rate. The stem relative growth rate was used to derive the array TCAN described below (Figure 41). The 18 to 23° C optimum temperature range for stem elongation is somewhat wider than that for stem growth. Both elongation and growth extrapolate to thermal maxima and minima of 30 and 0° C, respectively.

Root Growth

The root growth curves exhibit a form similar to the stem growth curves (Figure 38). The optimum temperature ranged from 20 to 22° C

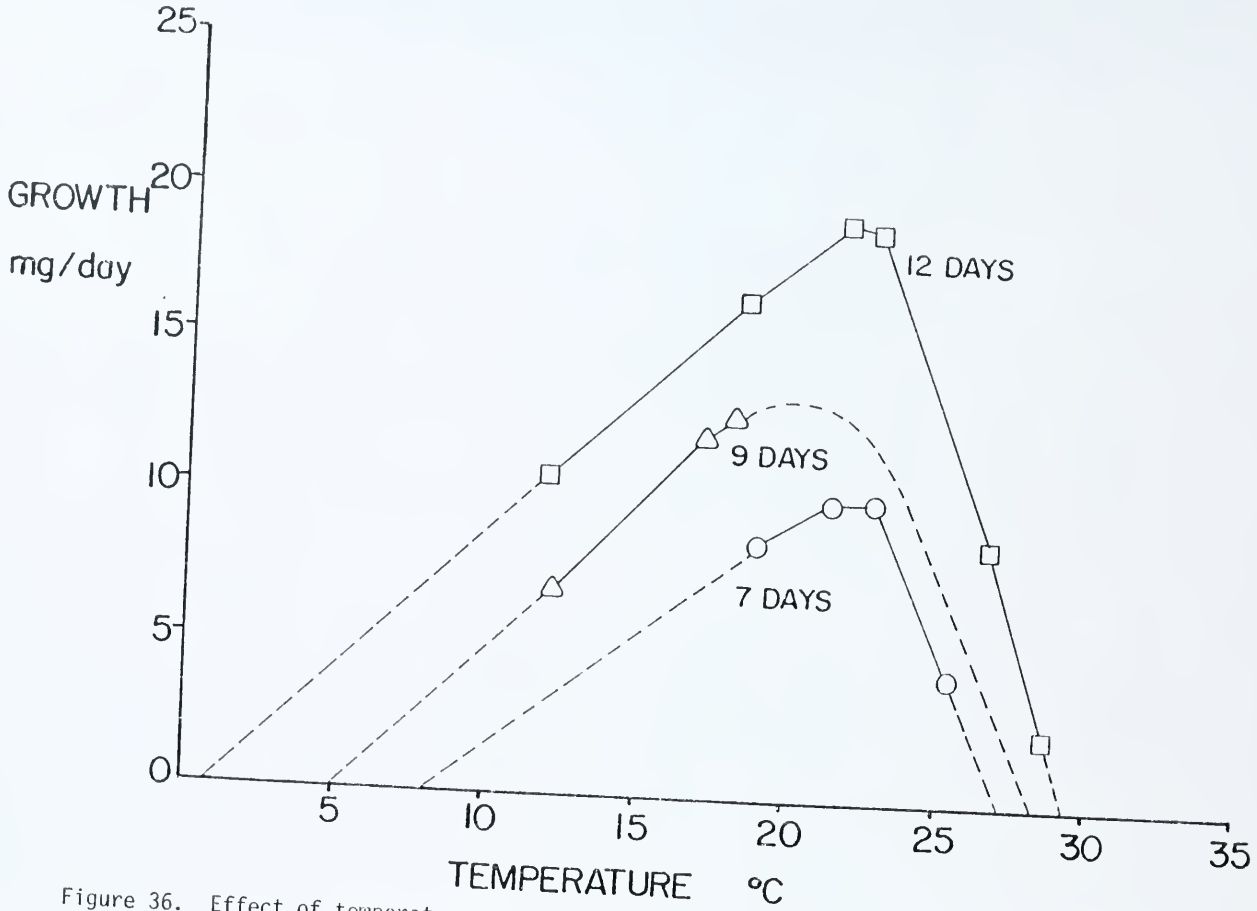

Figure 36. Effect of temperature on stem growth of Sebago potatoes with non-dormant buds. Growth measured after 7 (○), 9 (△), and 12 (□) days.

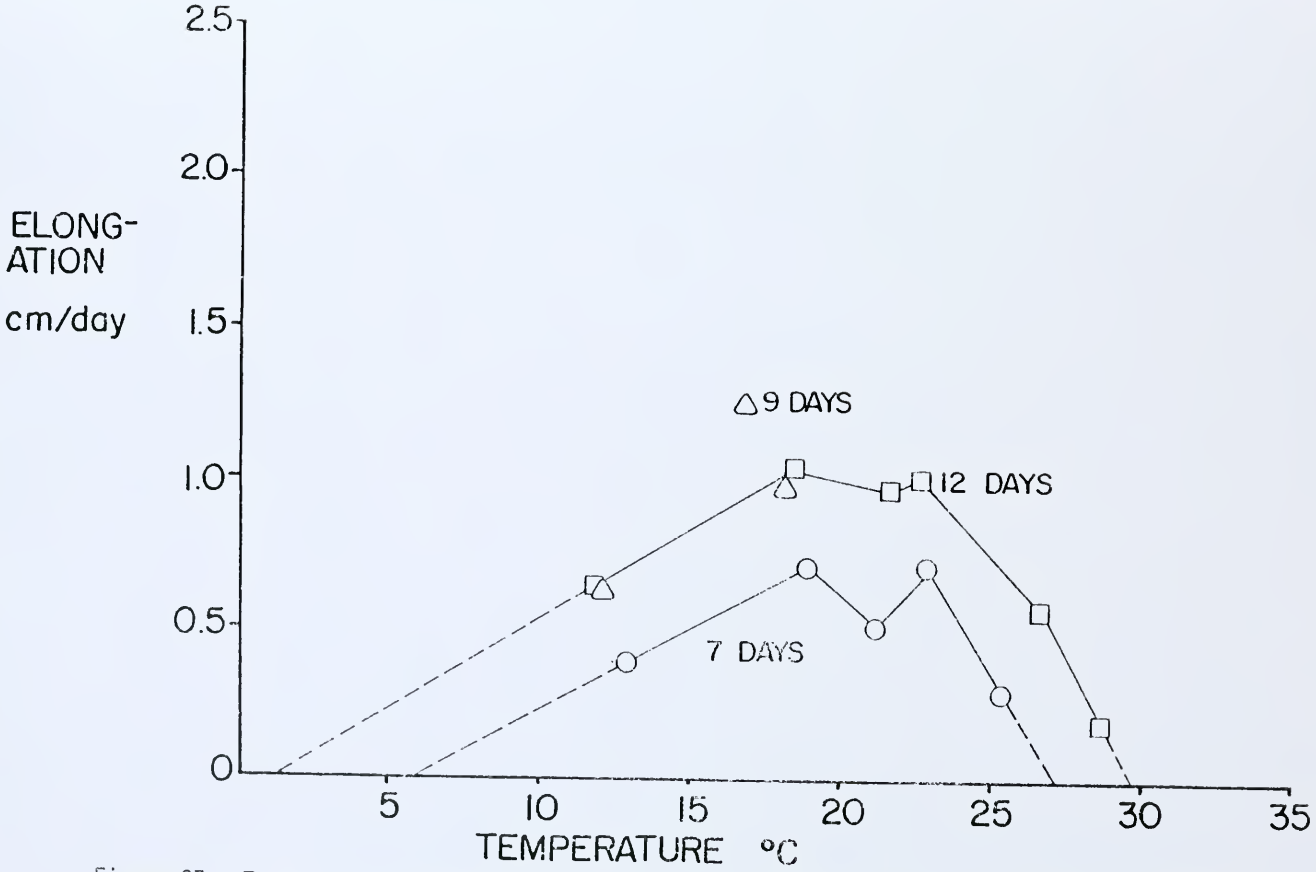

Figure 37. Temperature response for stem elongation in Sebago seed-pieces with non-dormant buds. Measured after 7 (○), 9 (△), and 12 (□) days.

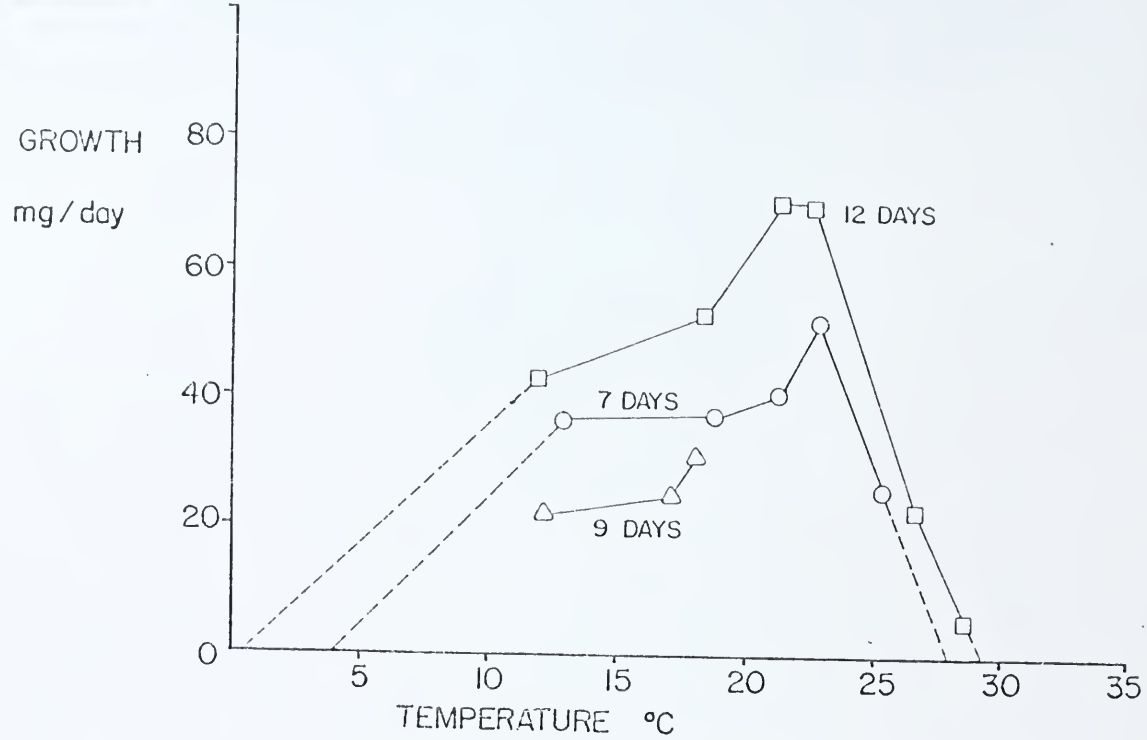

Figure 38. Root growth temperature response curves for Sebago potatoes.

with extrapolated maximum and minimum of 30 and 0° C, respectively. The root temperature relationship, however, seems to have a shoulder on the low temperature side of the optimum. The shoulder gives roots an even greater advantage over shoots at cooler temperatures. Note that the roots grew at a rate almost four times as fast as the stems at their respective optima.

The nine day curve for root growth appears misplaced. Since the seven and 12 day curves were generated by simultaneously growing plants they are presumed to show a true relationship to one another. They were used to develop an exponential relationship between root growth rate and time, thereby deriving another array, TROOT (Figure 41).

Tuber Growth

The temperature responses of tuber and total crop growth rates are graphed in Figure 39. These data were collected during the linear tuber growth phase. Therefore, the linear model used to calculate the growth rate is assumed to be correct and the data were used directly to derive the temperature response array TTUBR (Figure 42). The optimum temperature for tuber growth is around 15° C, much lower than the optima of root and stem growth. The calculated growth rates are twice as high as one would expect. The maximum crop growth rate for the field grown potatoes was about 21.5 g/m^2/day when corrected for incomplete ground cover. Furthermore, De Wit has shown that the potential growth rate for many crops and other plant life is about 20 g/m^2/day (McCloud, 1979). So a maximum total growth rate of 20 g/m^2/day is much more likely than the 40 g/m^2/day calculated.

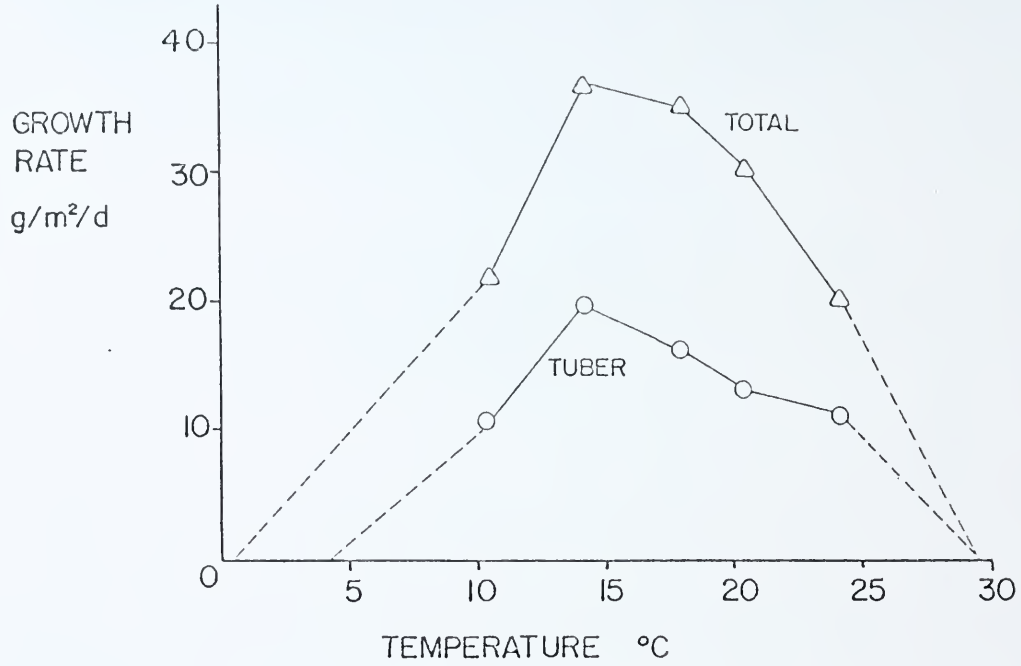

Figure 39. Effect of soil temperature on tuber and total growth rate of Sebago potatoes grown in 25 cm plastic pots.

Sebago Crop Growth Model

Though Monona yielded higher and seemed more adapted to Florida potato cultivation practices than Sebago according to the growth analysis, Sebago was chosen to be modeled and simulated. Sebago is more widely cultivated than Monona. Also, Sebago growth and development have been studied by several other workers so there is more information available on this cultivar. Furthermore, since the planting dates chosen for the growth analysis were the early and late extremes of the suggested planting period, Monona would out yield Sebago under more optimal conditons.

Model Development

A dry-matter flow diagram of the Sebago crop model is presented in Figure 40. Solid lines represent material flow and dashed lines represent information flow. Rectangles hold the dry-matter components of the model. Circular bubbles are input variables and clouds are unlimited sources or sinks. The last symbol is a labeled valve ( ) which represents a flow rate.

The model has three yield components, roots, tubers, and canopy, whose rates of growth depend upon temperature and the amount of substrate available for growth. If there is more carbohydrate available than these components can utilize, the extra substrate can be stored temporarily in a leaf pool which has a maximum size of 10% of the canopy dry weight. The model uses net rates, so respiratory losses from the yield components are implicit rather than explicit. The canopy does lose dry weight by senescence according to heat unit accumulation effects on leaf duration calculated in the growth analysis.

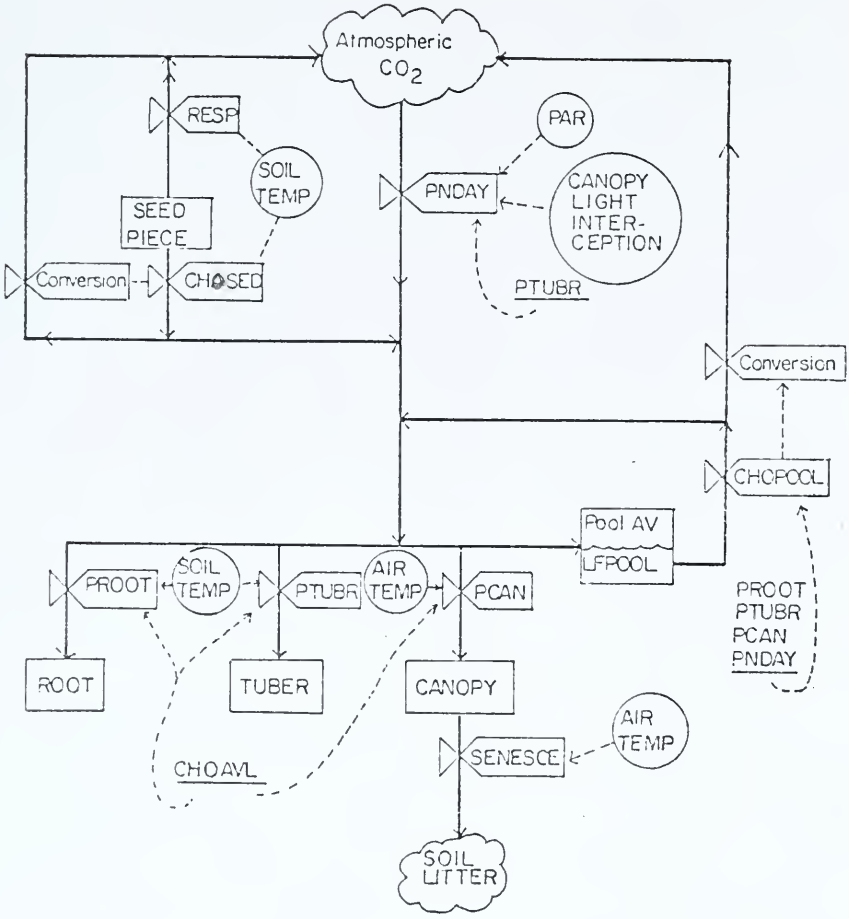

Figure 40. Dry-matter flow diagram for Sebago growth model. Variables defined in Appendix A, pages 130 and 132.

The growth substrate may come from the seed-pieces, photosynthesis, or the labile leaf carbohydrate storage pool. The carbohydrates coming from both the seed-pieces and the leaf pool show metabolic losses associated with translocation and conversion processes. The seed-pieces also lose dry weight through respiration which is governed by the soil temperature.

A two-phase linear model is used to describe the net photosynthetic light response curve:

$$\text{PNDAY} = \begin{cases} (0.04839*\text{PAR}) + 19.597 & \text{for PAR} \geq 30 \\ 0.7241*\text{PAR} & \text{for PAR} < 30 \end{cases}$$

where PNDAY is net photosynthesis in $g/m^2/day$ and PAR is photosynthetically active radiation in $E/m^2/day$. This model is similar to that of De Wit (1959) described above. The constants of this light response were calculated from Sale's (1974) work with Sebago potatoes grown in Australia. The two-phase linear model was chosen over a rectangular hyperbola because the two-phase linear model is simpler and because a slight change in the parameters of the rectangular hyperbola result in great changes in the estimated photosynthetic rate.

The light interception input uses ground cover data from the growth analysis. As will be seen below, inputting light interception rather than generating the photosynthetic surface internally is a major weakness of the model.

After tuber initiation net photosynthesis may be stimulated up to two-fold by the potential tuber growth rate. Photosynthetic enhancement by tubers was suggested in the literature and was found to be necessary for simulated growth values to approximate actual data.

Several temperature response curves have already been mentioned. A temperature response curve is used to predict or describe the effect of temperature on some process. The shapes of TCAN, TROOT, and TTUBR (Figures 41 and 42) were derived from thermogradient analysis and simulation trials. Each of these tables needed to be tested in the temperature range above the level of thermogradient analysis. The original extrapolations were found to underestimate growth in the 25 to 30° C range. The scales of these tables were determined from the growth analysis rather than the thermogradient analysis. For example, root growth was four times as fast as stem growth in the thermogradient analysis. The model, on the other hand, uses a faster canopy than root growth rate as shown in the growth analysis results. The adjustment was necessary because the temperature response curves were based upon growth when carbohydrate was not a limiting factor. To model post-emergence growth new relationships must be derived as the substrate supply becomes a limit to growth.

The amplitude of the TTUBR array was also reduced to correspond with the results of the growth analysis. To make these estimations from the growth analysis, the growth rate was calculated from the dry weight accumulation data and compared to the mean temperature during that period.

To generate the TUBRGR temperature response curve (Figure 41) the exponential growth phase from the growth analysis was used to determine the general range of tuber relative growth rates. Since there rates were about the same for the two plantings, a optimum plateau was modeled ranging from about 14 to 18° C.

All input tables are listed and defined with the model listing in Appendix A.

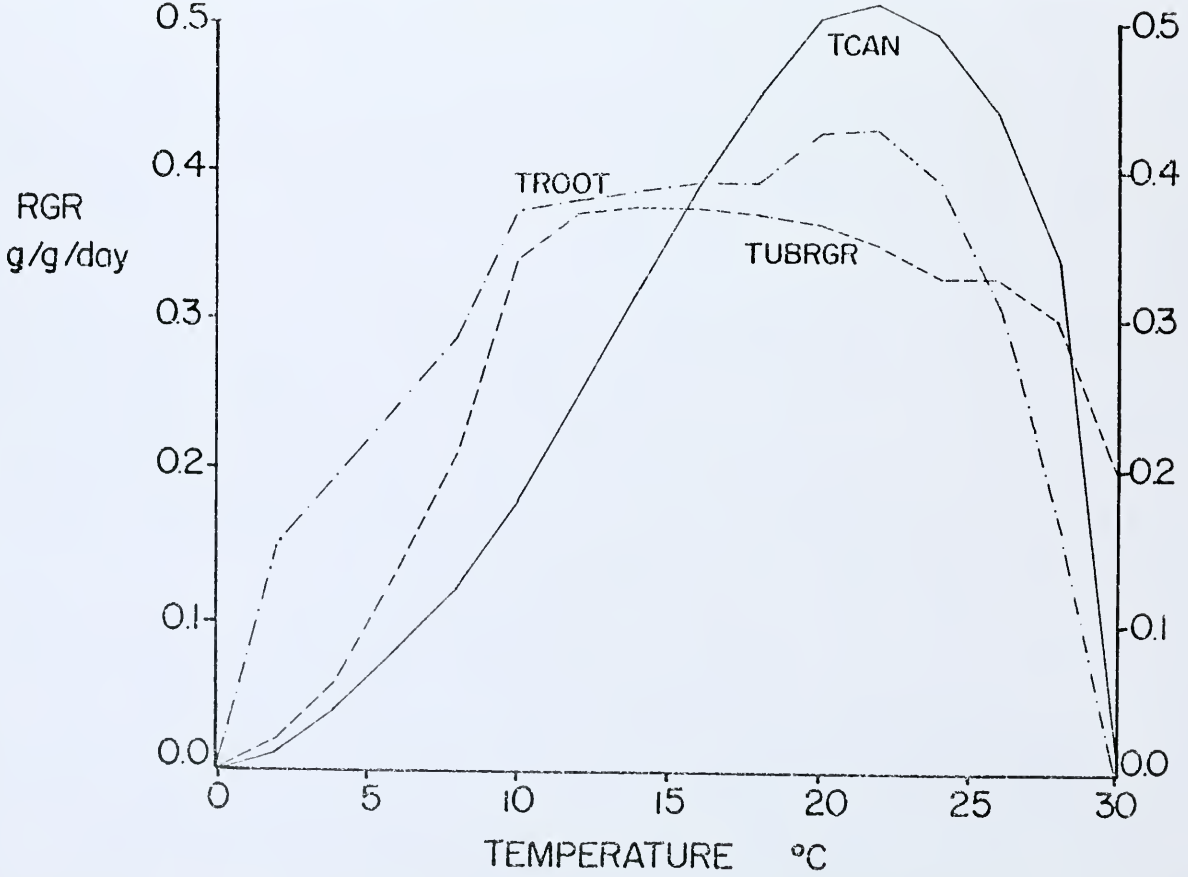

Figure 41. Relative growth rate vs. temperature for Sebago canopy (TCAN), roots (TROOT), and tubers (TUBRGR).

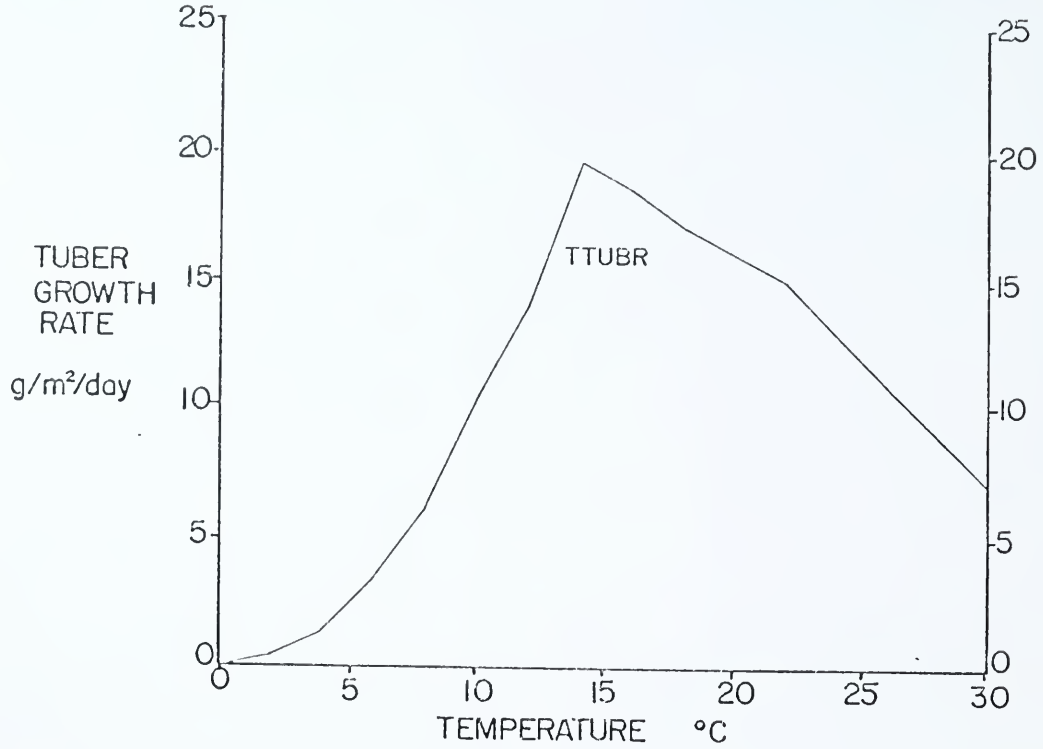

Figure 42. Tuber growth rate (TTUBR) vs. temperature for Sebago.

Model Validation

Models are validated by comparing simulated results with empirical observations. Tables 9 and 10 and Figures 43 and 44 compare real and simulated results of Sebago growth. For the Julian day 33 planting the simulated and field grown potatoes agree closely except during the 110 and 120 day period when the model over-estimates growth. The standard errors for tuber and total dry weights are 54.4 and 46.9 g/m^2, respectively. The model estimated the growth of the Julian day 73 planting more closely than the day 33 planting. The standard errors for tuber and total dry weight estimation in the day 73 planting are 18.0 and 17.2 g/m^2, respectively. The standard errors of the simulation are in the same range as the linear standard errors (Table 8).

The simulated tuber and crop growth rates and partitioning ratios in Table 11 can be compared to the growth analysis results in Table 8. The model over-estimates the crop growth rates of both planting dates and the tuber growth rate of the Julian day 73 planting. Still, the simulated growth rates and their ratios are close to the actual data. The tuber initiation dates calculated by exponential regression from the growth analysis were Julian day 84 and 116 for the Julian day 33 and 73 plantings, respectively. The model initiates tubers within two days of these dates.

At this point let me reiterate that every model, no matter how closely it estimates reality, is only a representation of reality. Too often, the mathematical or verbal symbols and concepts of a model are mistaken for reality because they are more easily understood than reality. Remembering that models are approximations of reality, at best, we analyze the results of this potato model.

Table 9. A post-emergence comparison of dry weights of field-grown and computer-simulated Sebago potatoes with a Julian Day 33 planting date.

Julian Day	Tubers		Total	
	Field Grown	Simulated	Field Grown	Simulated
	- - - - - - - - - - - - g/m^2 - - - - - - - - - - - -			
68			42.5	47.1
72			25.5	31.7
79			26.2	25.9
87	0.41	0.55	32.1	40.8
94	5.14	4.69	86.9	99.5
101	29.0	35.3	206.7	189.2
110	117.3	159.8	369.2	365.4
120	192.2	304.7	478.5	601.8
128	422.6	409.3	679.0	719.6
137	505.1	515.9	861.5	849.6

Table 10. A post-emergence comparison of dry weights of field-grown and computer simulated Sebago potatoes with a Julian Day 73 planting date.

Julian Day	Tubers		Total	
	Field Grown	Simulated	Field Grown	Simulated
	- - - - - - - - - - - - - g/m^2 - - - - - - - - - - - - -			
96			34.2	33.6
100			19.2	23.7
107			24.4	28.9
116	0.93	0.0	71.0	63.9
125	16.5	4.14	99.6	130.7
139	95.2	117.3	311.7	326.4
150	213.7	216.0	468.3	482.9

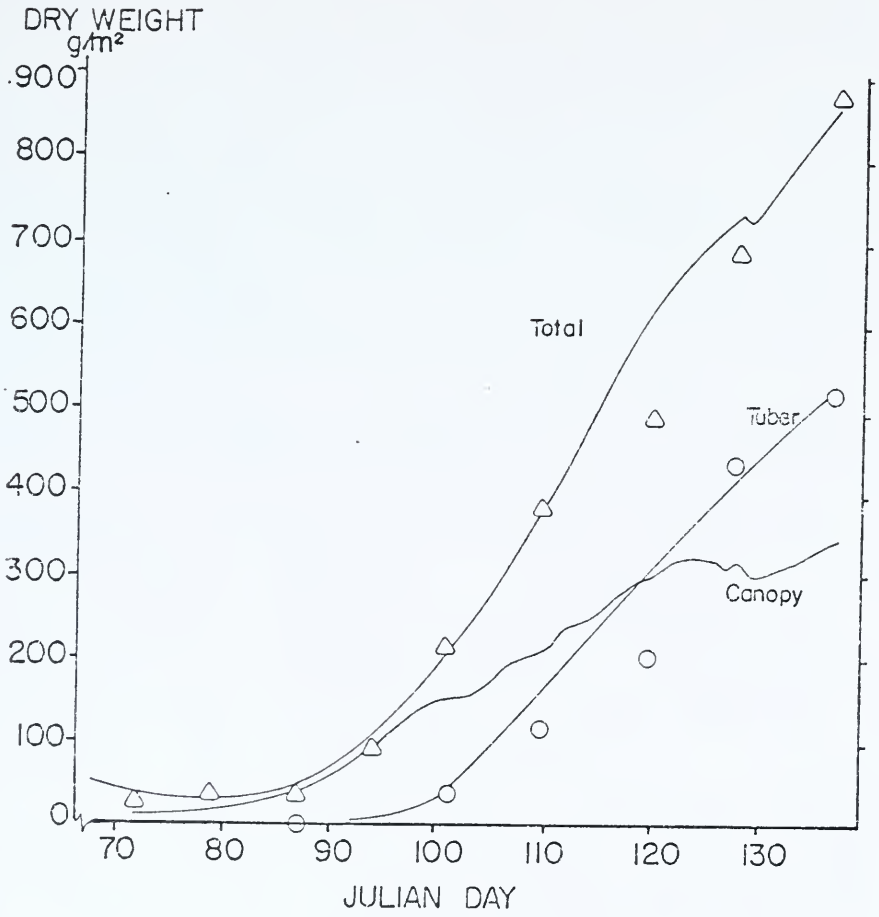

Figure 43. Simulated Sebago growth components with climatic inputs of the Julian day 33 growth analysis. Growth analysis data are plotted for total (○) and tubers (△).

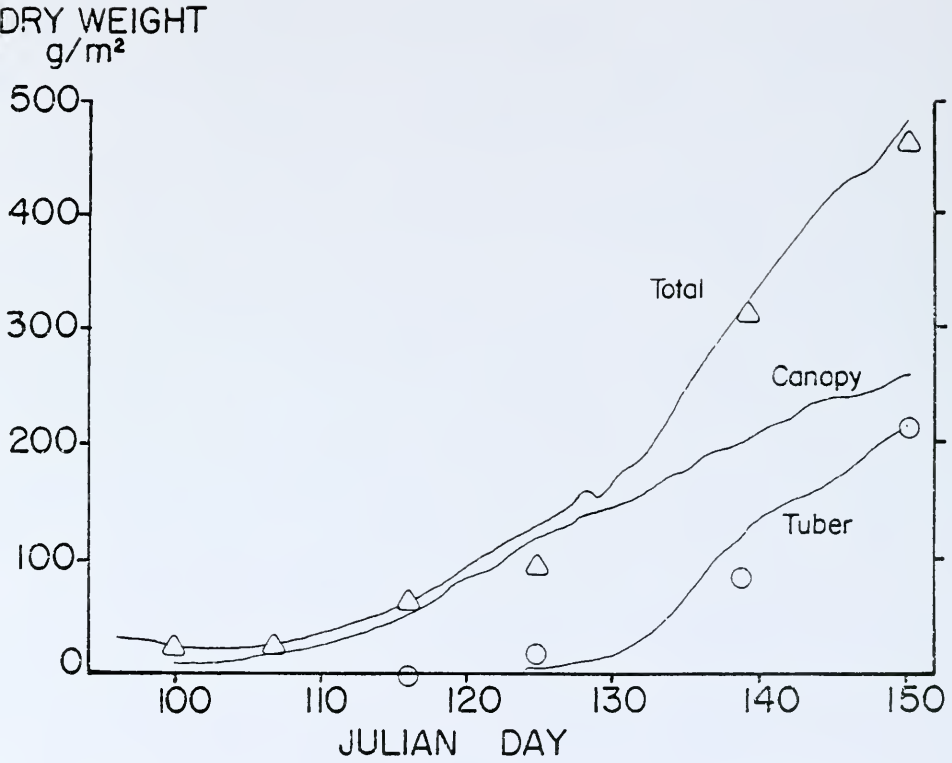

Figure 44. Simulated Sebago growth components with climatic inputs of the Julian day 73 growth analysis. Growth analysis data are plotted for total (○) and tubers (△).

Table 11. Simulated tuber and crop growth rates, assimilate partitioning ratio, and tuber initiation dates with climatic inputs of the Julian Day 33 and 73 growth analyses.

Climatic Inputs	TGR ± s.e.	CGR ± s.e.	TGR/CGR	Tuber Initiation
Julian Day	- - - - g/m^2/day - - - -			Julian Day
68-138	13.5 ± 0.082	18.7 ± 0.386	0.723	86
96-150	10.2 ± 0.182	15.3 ± 0.542	0.669	117

Temperature Sensitivity Analysis

The results of a temperature sensitivity analysis of the Sebago crop growth model are presented in Tables 12 through 15. In addition to the tuber and crop growth rates and their ratio, the crop growth model allows analysis of net photosynthesis. All of the rates in Tables 12 and 13 were computed over the linear tuber growth period. The net photosynthesis rates during the linear tuber growth period are about double the rate prior to tuber initiation as one would expect from the influence of the model variable STIM, which acts to increase photosynthesis during tuber growth.

The difference between daily net photosynthesis in the various temperature treatments is insignificant. The lack of temperature effect on net photosynthesis may be taken as confirmation of Sale's (1974) finding that temperature did not influence net carbon exchange in the field. However, since this model does not generate its own photosynthetic surface one would not expect great differences between treatments. Any differences in photosynthesis between the treatments are indirect reflections of the effect of soil temperature on tuber growth.

The net photosynthetic rates do differ markedly from the crop growth rates. In growth analyses the crop growth rate is often considered an estimator of net canopy photosynthesis. This model, which accounts for canopy senescence throughout the season, shows the potential error of using dry-matter accumulation to estimate net photosynthesis. At cool air temperatures, when leaf duration is prolonged, the crop growth rate closely approximates net photosynthesis.

Table 12. Simulated tuber and crop growth rates, mean daily net photosynthesis, and photosynthate partitioning ratios for various temperature inputs. All calculations from linear tuber growth phase.

Temperature						
Soil	Air	TGR	CGR ± s.e.	PNDAY ± s.d.	TGR/CGR	TGR/PNDAY
- - °C - -		- - - - - $g/m^2/day$ - - - - - - - - - -				
20	25	16.3	20.2 ± 0.06	31.0 ± 0.97	0.81	0.52
15	25	18.9	21.8 ± 0.13	32.1 ± 1.92	0.87	0.59
15	20	19.1	23.4 ± 0.07	32.9 ± 0.73	0.82	0.58
10	20	10.4	15.3 ± 0.08	26.7 ± 1.29	0.68	0.39
20	15	16.0	25.0 ± 0.25	32.3 ± 1.50	0.64	0.50
25	15	12.0	19.7 ± 0.26	29.1 ± 0.85	0.61	0.41

Table 13. Simulated tuber and crop growth rates, mean daily net photosynthesis, and photosynthate partitioning ratios for various temperature inputs. All calculations from linear tuber growth phase.

Temperature						
Soil	Air	TGR ± s.e.	CGR ± s.e.	PNDAY ± s.d.	TGR/CGR	TGR/PNDAY
- - °C - -		- - - - - - - - -	g/m^2/day - - - - - - - - -			
10	10	10.5	26.5 ± 0.20	26.9 ± 1.5	0.40	0.39
15	15	19.1	26.1 ± 0.15	32.3 ± 1.7	0.73	0.59
20	20	16.0	21.3 ± 0.10	32.0 ± 0.7	0.75	0.50
25	25	12.7	14.4 ± 0.70	28.1 ± 3.5	0.88	0.45
30→10	30→10	14.0 ± 0.302	25.2 ± 0.27	30.8 ± 1.9	0.56	0.45
10→30	10→30	12.3 ± 0.216	16.9 ± 0.35	30.0 ± 2.5	0.73	0.41

Table 14. Simulated final yields for tubers, canopy, roots, and total and tuber initiation dates with various temperature inputs.

Temperature		Dry Weight				Tuber
Soil	Air	Tubers	Canopy	Roots	Total	Initiation
- - - ° C - - -		- - - - - - - - g/m^2 - - - - - - - -				Julian Day
10	10	409	758	4.62	1,172	87
15	15	791	382	3.64	1,177	83
20	20	602	351	3.78	957	81
25	25	123	315	5.98	443	115
30 → 10	30 → 10	251	484	5.44	741	108
10 → 30	10 → 30	514	335	3.91	853	84

Table 15. Simulated final yields for tubers, canopy, roots, and total and tuber initiation dates with various temperature inputs.

Temperature		Dry Weight				Tuber
Soil	Air	Tubers	Canopy	Roots	Total	Initiation
- - - ° C - - -		- - - - - - - - g/m^2 - - - - - - - -				Julian Day
10	20	409	356	3.76	769	87
15	20	712	313	3.75	1,030	87
15	25	179	305	5.96	490	115
20	25	156	311	5.98	473	115
20	15	664	459	3.72	1,155	83
25	15	498	467	3.80	970	83

At warm air temperatures canopy development is hastened and the crop growth rate is a poor estimator of net photosynthesis.

When soil and air temperature inputs are equal, 15° C is optimum for tuber and total growth. The 15° C temperature regime had a high tuber growth rate and early tuber initiation which combined to give the greatest yield of all treatments. The 10° C treatment had a total yield almost equal to that of the 15° C treatment and also had early tuber initiation. The tuber growth rate of the 10° C condition was about half the rate of the 15° C treatment and the resultant yield was about half as great in the 10 as the 15° C treatment. At 25° C the warm temperature delayed tuber initiation until Julian day 115 and greatly reduced the tuber and crop growth rates. As well as being above the optimum temperatures for tuber and crop growth, the 25° C input hastened canopy senescence to reduce crop growth further.

The effects of steadily increasing and decreasing temperatures on Sebago growth and development may be compared to spring and fall crops, respectively. As with the seasonal comparison of Australian potatoes by Moorby and Milthorpe (1975), the simulated increasing temperature treatment yielded greater than the decreasing temperature treatment. The higher yield in the increasing temperature treatment occurred despite lower tuber and crop growth rates. The yield advantage in the increasing temperature condition results from earlier tuber initiation. Tubers initiated 24 days sooner when temperatures were increasing than when decreasing. This result is similar to the conclusions of Moorby and Milthorpe's analysis.

The daily mean air and upper soil layer temperatures do not differ greatly. Still, by inputting different soil and air temperatures into

a model one can test their relative effects on model functioning. The primary effect of air temperature appears to be on the rate of tuber initiation. At a soil temperature of 15° C, the tuber yield was about three times higher with an air temperature of 20° C than 25° C due to a 28 day delay of tuber initiation at the high air temperature. The soil temperature seems to have its major effect on the tuber growth rate. For equal air temperatures, the tuber initiation date will be the same. The soil temperature will determine yield in this case with the optimum temperature of 15° C. In the 10° C soil and 20° C air temperature condition another factor may be involved. At this soil temperature the tuber growth rate may be low enough that the stimulatory effect of tubers on photosynthesis is either diminished or delayed. The very low tuber and crop growth rates and slightly lower net photosynthetic rate suggest this possibility. Still, tubers were initiated early giving a long tuber growth period and a respectable final tuber yield.

The two simulations with soil temperature exceeding air temperature also show the effect of tuber growth on crop growth. At high soil temperature both tuber and crop growth are reduced. Since the air temperature and therefore the canopy senescence rates are equal, the reduction of crop growth rate must be through a reduction of the photosynthetic enhancement by tubers.

In potatoes, photosynthate partitioning is a dynamic process relating tuber and haulm growth. The common means of estimating assimilate partitioning to the yield organ is by the ratio of yield and crop growth rates (Duncan et al., 1978). As noted above, potatoes offer an excellent opportunity to examine assimilate partitioning

because the tuber and haulm growth periods generally coincide. However, since the crop growth rate includes canopy loss through senescence, a more accurate estimation of assimilate partitioning to tubers is the ratio of the tuber growth rate to daily net photosynthesis. Both of these ratios are given in Tables 12 and 13.

Even though the tuber growth rate to net photosynthesis ratio conforms to the physiologic definition of assimilate partitioning, this ratio does not aid interpretation of this potato growth and development model. Since the net photosynthesis did not differ significantly between treatments, the partitioning ratio followed the same trends with temperature as the tuber growth rate. Here again is the need for an internally generated photosynthetic surface.

The tuber growth rate to crop growth rate ratio, on the other hand, does show an interesting response to temperature. Most notable is the increase of the TGR to CGR ratio with an increase in temperature where soil and air temperature inputs are equal. The simulated potato plants in the increasing temperature regime partitioned more assimilate to tubers than canopy in the decreasing temperature regime. In the increasing temperature condition, the temperatures are warm during the tuber growth period while the converse is true in the decreasing temperature condition. Thus these gradual temperature changes show a similar response with greater partitioning when tubers grow in warmer conditions.

SUMMARY AND CONCLUSIONS

Growth Analysis

The warmer soil temperatures of the Julian day 73 planting speeded shoot elongation and decreased the shoot to root ratio up to the time of emergence.

In both plantings, Monona achieved a higher seed-piece emergence than Sebago. The Julian day 33 seed-piece emergence was greater than that of the Julian day 73 planting for both cultivars.

In both plantings Sebago flowered more profusely and persistently than Monona.

The Sebago canopy developed more slowly than that of Monona in the Julian day 73 planting. Still, Sebago's canopy reached and maintained a higher LAI and ELAI than Monona in both plantings.

Sebago grew more and longer branches than Monona in the Julian day 33 planting while there were no differences in branching between the cultivars in the Julian day 73 planting. The canopies of both cultivars reached maximum branch length more quickly in the Julian day 73 planting and these branch lengths were shorter in the second planting.

Monona had a slightly longer leaf duration than Sebago in both plantings. The leaf duration of the Julian day 33 planting was greater for both cultivars than the leaf duration of the canopies in the Julian day 73 planting.

Days to emergence and from emergence to flowering both have a positive relationship to cummulative heat units while the time from emergence to tuber initiation is negatively related to heat unit accumulation.

Both cultivars exhibited a period of zero crop growth during which dry weight was apparently transferred from the seed-pieces to the canopy. The exponential growth phase was very short. These cultivars shifted rapidly from the zero to linear growth.

Monona had a higher tuber yield than Sebago in both plantings although total yields were similar for the two cultivars. Monona partitioned more photosynthate into tuber growth than did Sebago. The yield and assimilate partitioning to tubers were greater in the Julian day 33 planting than the Julian day 73 planting for both cultivars.

Thermogradient Analysis

The optimum temperature for Sebago bud dormancy break was from 18 to 24° C.

The optimum temperature range for stem elongation was 20 to 22° C while that for stem elongation was 18 to 23° C.

The optimum temperature for root growth was from 20 to 22° C. The root growth temperature response curve showed a shoulder to 12° C below the optimum temperature while shoot growth and elongation both declined steadily above and below their thermal optima.

The optimum temperature for tuber growth was from 14 to 17° C. The optimum temperature for total crop growth followed the pattern for tuber growth during the linear tuber growth phase.

Sebago Crop Growth Model

The simulation model more closely estimated the growth and development of the Julian day 73 planting than the Julian day 33 planting. The standard errors of estimating the two plantings were approximately 18 and 50 g/m^2, respectively.

There was little difference in daily net photosynthesis in the temperature regimes tested, presumably because light interception was an input variable rather than being calculated within the model.

The optimum temperature regime for tuber and total yield was with both air and soil temperature equal to 15° C.

The major effect of soil temperature on Sebago growth was through the tuber growth rate. A secondary effect was through the effect of tuber growth rate on the photosynthetic rate. At sub- or supra-optimal soil temperatures both the tuber and photosynthetic rates were reduced with the tuber growth rate being the more sensitive to temperature.

The major effect of air teperature was on the tuber initiation rate. Warm air temperatures delayed tuber initiation and reduced the tuber growth period.

An increasing temperature environment was shown to be more favorable for potato production than a decreasing temperature environment of equal mean temperature. Tubers initiated earlier in the increasing temperature condition giving a longer tuber growth period.

When using the net daily photosynthetic rate to calculate the partitioning to tubers the partitioning ratio follows the same pattern as the tuber growth temperature response. When the crop growth rate is used to calculate the partitioning ratio the partitioning ratio increased with temperature.

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APPENDIX A:

LISTING OF VARIABLE DEFINITIONS, MODEL PROGRAM, COMMON BLOCK VARIABLES, INPUT TABLES, INITIAL VALUES OF STATE VARIABLES, AND PLOT STATEMENT FILES OF THE SEBAGO GROWTH AND DEVELOPMENT MODEL

VARIABLE DEFINITIONS FOR POTATO GROWTH MODEL

ATRIB(I): A GASP IV variable used to store information in files NSET and QSET. ATRIB(1) = event time; ATRIB(2) = event number; ATRIB(3) = DCAN (SEE); ATRIB(4) = heat unit accumulator for canopy senescence.

BULK: A flag which denotes exponential tuber growth when less than 1.0 or linear when equal to 1.0.

BULKMN: The minimum potential tuber growth necessary to initiate linear tuber growth.

CAN (g/m^2): The dry weight of the potato canopy.

CANGRO ($g/g/m^2$): Relative canopy growth rate.

CHOAV (g/m^2): Carbohydrate available for canopy and root growth.

CHODAY (g/m^2): Total amount of carbohydrate available each day.

CHOSED (g/m^2): Carbohydrate available from seed-piece for growth.

CHOTOT (g/m^2): Carbohydrate available for total crop growth.

DCAN (g/m^2): The amount by which the canopy is reduced after energy heat units are accumulated in ATRIB(4).

EXCESS (g/m^2): Quantity of photosynthate above that which can enter a days growth or the carbohydrate pool in leaves.

EXTRA (g/m^2): Quantity of photosynthate above that which can enter daily growth.

FILEM(I): A GASP IV function used to file events.

GCI (%): The ground cover for a particular day.

GCSE1: A table of ground cover for SE1.

GCSE2: A table of ground cover for SE2.

JDAY: Julian Day

LFPOOL (g/m^2): Amount of carbohydrate stored in the leaf pool.

MNPOOL (g/m^2): Minimum stored carbohydrate level which stimulates tuber initiation.

MNTUBR (g/m^2): Minimum tuber growth rate for linear growth (bulking).

MXGRO (g/m^2): Maximum growth of crop organs.

MXPOOL (g/m^2): Maximum size of leaf pool 10% of CAN.

NCRDR: Number of the card reader for I/O.

NPRNT: Number of printer for I/O.

NSET(I): A GASP IV array used to store file data.

PAR (E/m^2): Daily photosynthetically active radiation.

PCAN (g/m^2): Potential canopy growth as temperature response.

PDMND (g/m^2): Photosynthate demand by crop organs.

PLOT(I): GASP IV variables used in plotting function.

PN(I) (g/m^2): Daily photosynthetic production used for calculating a three day average.

PNAVE (g/m^2): Three day average for photosynthesis.

PNDAY (g/m^2): Daily photosynthate.

PNMAX (g/m^2): Potential daily photosynthesis as determined by PAR and GCI.

POOLAV (g/m^2): Space available in MXPOOL for excess daily photosynthesis.

PROOT (g/m^2): Potential root growth.

PROOT2 (g/m^2): Potential root growth when sink demand exceeds photosynthate supply.

PTUBR (g/m^2): Potential tuber growth.

QSET(I): GASP IV array used like NSET(I).

ROOT (g/m^2): Root biomas dry weight.

RTGRO ($g/g/m^2$): Relative root growth rate.

SEED (g/m^2): Seed biomass dry weight.

SEEDMX (g/m^2): Variable used to determine the amount of seed dry weight available for daily growth. Dry weight available for daily growth.

STIM: A factor by which photosynthesis is stimulated by potential tuber growth.

TAIR (Deg. C): Air temperature.

TAMAX (Deg. F): Daily maximum air temperature.

TAMIN (Deg. F): Daily minimum air temperature.

TCAN: Table of canopy relative growth rate vs. temperature.

TINIT: A flag indicating that tubers have not (less than 1.0) or have (1) been initiated.

TOTAL (g/m^2): Total crop biomass dry weight.

TROOT: Table of root relative growth rate vs. temperature.

TSEED: Table of seed CHO available vs. temperature.

TSMAX (Deg. F): Daily maximum soil temperature.

TSMIN (Deg. F): Daily minimum soil temperature.

TSOIL (Deg. C): Daily average soil temperature.

TTUBR: Table of tuber growth vs. temperature.

TUBGR (g/m^2): Daily tuber growth.

TUBGRO ($g/g/m^2$): Relative tuber growth rate.

TUBR (g/m^2): Tuber biomass dry weight.

TUBRGR: Table of tuber relative growth rate vs. temperature.

SEBAGO GROWTH AND DEVELOPMENT MODEL

```
 //POTATO JOB (1001,1401,5,10),'KINGRAM',CLASS=2
 /*PASSWORD
 /*ROUTE  PRINT TCP
 // EXEC GASPIV,PARM='NOMAP,NOSOURCE'
 //FORT.SYSIN DD *
       BLOCK DATA
 /*INCLUDE COMMON
 /*INCLUDE TABLES
       END
 /*INCLUDE COMMON
       DIMENSION NSET(2000)
       COMMON QSET(2000)
       EQUIVALENCE (NSET(1),QSET(1))
       NCRDR=5
       NPRNT=6
       CALL GASP
       STOP
       END
C
C   INTLC IS THE SYSTEM INITIALIZATION SUBROUTINE. DEFINITIONS
C   FOR ALL VARIABLES USED HERE AND IN THE REST OF THE
C   PROGRAM ARE LISTED IN THE FILE NAMED VARIABLE.
C
       SUBROUTINE INTLC
 /*INCLUDE COMMON
 /*INCLUDE SE1
       LFPOOL=0.
       TINIT=0.
       PTUBR=0.
       BULKMN=10.
       PN(1)=0.
       PN(2)=0.
       PN(3)=0.
       BULK=0
       RETURN
       END
C
C   EVNTS(IX) IS A SUBROUTINE WHICH CALLS THE VARIOUS
C   EVENT SUBROUTINES SCHEDULED AND STORED IN NSET
C   BY THE CALL FILEM(1) STATEMENT.  THE DESCRIPTIONS
C   OF THE FIVE EVENTS PRECEDE EACH OF THESE SUBROUTINES.
C
       SUBROUTINE EVNTS(IX)
       GO TO (1,2,3,4,5,6),IX
     1 CALL PRET
       GO TO 800
     2 CALL POSTT
       GO TO 800
     3 CALL CANDE
       GO TO 800
     4 CALL DAY
       GO TO 800
     5 CALL ENDAY
       GO TO 800
     6 CONTINUE
   800 RETURN
       END
C
C   THE DAY SUBROUTINE READS THE CLIMATIC DATA, CONVERTS
C   AIR AND SOIL TEMPERATURES FROM DEG F TO DEG C, CAL-
```

SEBAGO GROWTH AND DEVELOPMENT MODEL

```
C   CULATES THE CARBOHYDRATE AVAILABLE FROM PHOTOSYNTHESIS
C   AND THE SEED-PIECE, AND SCHEDULES A CROP GROWTH EVENT.
C   NOTE THAT LIGHT INTERCEPTION IS GREATER THAN GROUND
C   COVER DURING EARLY GROWTH.  THIS INCREASES PNDAY.
C   ALSO, THE POTENTIAL TUBER GROWTH RATE (PTUBR) IS USED
C   TO STIMULATE AN INCREASE IN PHOTOSYNTHESIS DURING THE
C   TUBER GROWTH PERIOD.
C
      SUBROUTINE DAY
 /*INCLUDE COMMON
      READ(5,100)JDAY,PAR,TAMAX,TAMIN,TSMAX,TSMIN
  100 FORMAT (F3.0,1X,F3.1,1X,F2.0,1X,F2.0,1X,F2.0,1X,F2.0)
      TSOIL=((((TSMIN+TSMAX)/2.)-32.)*5.)/9.
      TAIR=((((TAMIN+TAMAX)/2.)-32.)*5.)/9.
      IF(PAR.LT.30.) PNMAX=0.7241*PAR
IF(PAR.GE.30.)PNMAX=(0.04839*PAR)+19.597
      GCI=GTABL(GCSE1,JDAY,68.,138.,5.)
      LI=GCI*(0.75+((100.-GCI)/100.))
      STIM=(PTUBR/BULKMN)+1.
      IF(STIM.GT.2.) STIM=2.
      PNDAY=((PNMAX*LI)/100.)*STIM
      SEEDMX=GTABL(TSEED,TSOIL,0.,28.,2.)
      CHOSED=((SEED-10.)/40.)*SEEDMX
      IF(SEED.LE.10.) CHOSED=0.
      CHOTOT=CHOSED+PNDAY+LFPOOL
      MXPOOL=CAN*0.1
      POOLAV=MXPOOL-LFPOOL
      SEED=SEED-(SEED*((0.0055*TSOIL)-0.0123))
      IF (TUBR.GT.0.) GO TO 14
      ATRIB(2)=1
      ATRIB(1)=JDAY
      CALL FILEM(1)
      GO TO 15
   14 ATRIB(2)=2
      ATRIB(1)=JDAY
      CALL FILEM(1)
   15 CONTINUE
      RETURN
      END
C
C   THE PRET SUBROUTINE IS USED TO CALCULATE GROWTH AND
C   PARTITIONING DURING THE INITIAL CROP GROWTH PHASE.
C   POTENTIAL GROWTH RATES ARE CALCULATED BASED UPON
C   TEMPERATURE.  THESE ARE COMPARED TO THE CHO AVAILABLE
C   FOR GROWTH.  IF POTENTIAL GROWTH IS GREATER THAN THE
C   CHO AVAILABLE THE CHO IS PARTITIONED ACCORDING TO
C   THE SINK DEMAND (TAKEN TO BE RELATED TO POTENTIAL
C   GROWTH) AND THE MASS OF THE SINK.  IF THERE IS EXCESS
C   CHO AVAILABLE (EXTRA) THIS IS EITHER PLACED IN A
C   LEAF POOL IF SPACE IS AVAILABLE IN THE POOL, OR
C   PHOTOSYNTHESIS IS REDUCED AS BY FEEDBACK INHIBITION.
C
      SUBROUTINE PRET
 /*INCLUDE COMMON
      ROOT=ROOT+0.1
      CANGRO=GTABL(TCAN,TAIR,0.,30.,2.)
      PCAN=CAN*CANGRO
      CHODAY=(CHOSED*0.7692)+PNDAY-0.1
      CHOAVL=CHODAY+(LFPOOL*0.7692)
      IF(PCAN.GT.CHOAVL)GO TO 20
```

```
      CAN=CAN+PCAN
      DCAN=PCAN
      IF(PCAN.GT.CHODAY)GO TO 21
      EXTRA=CHODAY-PCAN
      IF(EXTRA.GT.POOLAV)GO TO 22
      LFPOOL=LFPOOL+EXTRA
      SEED=SEED-CHOSED
      DEBUG=1.
      GO TO 23
   22 LFPOOL=LFPOOL+POOLAV
      EXCESS=EXTRA-POOLAV
      SEED=SEED-CHOSED+EXCESS
      DEBUG=2.
      GO TO 23
   21 SEED=SEED-CHOSED
      LFPOOL=LFPOOL-(1.3*(PCAN-CHODAY))
      DEBUG=3.
      GO TO 23
   20 CAN=CAN+CHOAVL
      DCAN=CHOAVL
      SEED=SEED-CHOSED
      LFPOOL=0.
      DEBUG=4.
   23 TINIT=TINIT+GTABL(T8IZE,TAIR,2.,28.,2.)
      IF(TINIT.LT.1.)GO TO 25
      TUBR=0.4
      WRITE(6,200)JDAY
  200 FORMAT('0','***** TUBERS INITIATED ON JULIAN DAY',1X,
     &F5.0,1X,'*****')
   25 CONTINUE
      TOTAL=CAN+ROOT+SEED
   28 ATRIB(1)=JDAY+1.
      ATRIB(2)=3
      ATRIB(3)=DCAN
      ATRIB(4)=(0.00423*TAIR)-0.032
      CALL FILEM(1)
      ATRIB(1)=JDAY
      ATRIB(2)=5
      CALL FILEM(1)
      RETURN
      END
C
C   THE POSTT SUBROUTINE CALCULATED GROWTH AND PARTITIONING
C   DURING THE TUBER GROWTH PHASES (BOTH EXPONENTIAL AND
C   LINEAR) OF CROP DEVELOPMENT.  A THREE DAY AVERAGE OF
C   PHOTOSYNTHESIS IS USED TO DETERMINE WHEN THE LINEAR
C   PHASE OF TUBER GROWTH IS REACHED.  WHEN TUBER GROWTH
C   REACHES 70 PERCENT OF THE THREE DAY AVERAGE OF PHOTO-
C   SYNTHESIS THE LINEAR PHENOPHASE IS INITIATED.  AS IN
C   THE PRET SUBROUTINE, THE CHO AVAILABLE FOR GROWTH IS
C   COMPARED TO THE POTENTIAL ORGANS GROWTH AND THE POOL
C   SPACE AVAILABLE.  THE TUBERS HAVE ULTIMATE PRIORITY
C   FOR CARBOHYDRATE AND WILL REDUCE THE CANOPY AND ROOT
C   DRY WEIGHTS IF NECESSARY.
C
      SUBROUTINE POSTT
 /*INCLUDE COMMON
      CANGRO=GTABL(TCAN,TAIR,0.,30.,2.)
      PCAN=CAN*CANGRO
      PROOT=0.1
```

SEBAGO GROWTH AND DEVELOPMENT MODEL

```
      MXGRO=PROOT+PCAN
      IF(BULK.GE.1)GO TO 35
      TUBGRO=GTABL(TUBRGR,TSOIL,0.,30.,2.)
      PTUBR=TUBR*TUBGRO
      BULKMN=PNAVE*0.7
      IF(PTUBR.GT.BULKMN)GO TO 34
      TUBR=TUBR+PTUBR
      CHODAY=PNDAY+(CHOSED*0.7692)-PTUBR
      CHOAVL=CHODAY+(LFPOOL*0.7692)
      IF(MXGRO.GT.CHOAVL)GO TO 30
      CAN=CAN+PCAN
      TUBR=TUBR+PTUBR
      DCAN=PCAN
      IF(MXGRO.GT.CHODAY)GO TO 31
      EXTRA=CHODAY-MXGRO
      IF(EXTRA.GT.POOLAV) GO TO 32
      LFPOOL=LFPOOL+EXTRA
      SEED=SEED-CHOSED
      DEBUG=5.
      GO TO 33
   32 LFPOOL=LFPOOL+POOLAV
      SEED=SEED-CHOSED+EXTRA-POOLAV
      DEBUG=6.
      GO TO 33
   31 LFPOOL=LFPOOL-(1.3*(MXGRO-CHODAY))
      SEED=SEED-CHOSED
      DEBUG=7.
      GO TO 33
   30 LFPOOL=0.
      ROOT=ROOT+((PROOT/MXGRO)*CHOAVL)
      CAN=CAN+((PCAN/MXGRO)*CHOAVL)
      SEED=SEED-CHOSED
      DCAN=(PCAN/MXGRO)*CHOAVL
      DEBUG=8.
      GO TO 33
   34 TUBR=TUBR+BULKMN
      BULK=BULK+1
      CHOAVL=(PNDAY-BULKMN)+((CHOSED+LFPOOL)*0.7692)
      CAN=CAN+((PCAN/MXGRO)*CHOAVL)
      ROOT=ROOT+((PROOT/MXGRO)*CHOAVL)
      DCAN=(PCAN/MXGRO)*CHOAVL
      LFPOOL=0.
      SEED=SEED-CHOSED
      DEBUG=9.
      GO TO 33
   35 PTUBR=GTABL(TTUBR,TSOIL,0.,30.,2.)
      TUBR=TUBR+PTUBR
      IF(PTUBR.GT.PNDAY)GO TO 36
      IF(PTUBR.GT.(0.8*PNDAY))GO TO 37
      CHOAVL=PNDAY-PTUBR
      DEBUG=10.
      GO TO 38
   37 CHOAVL=0.2*PNDAY
      DEBUG=11.
      GO TO 38
   36 PNDAY=PNDAY+(0.25*PNDAY)
      CHOAVL=PNDAY-PTUBR
      DEBUG=12.
   38 CONTINUE
      CAN=CAN+((PCAN/MXGRO)*CHOAVL)
```

SEBAGO GROWTH AND DEVELOPMENT MODEL

```
      IF(CHOAVL.LT.0.)GO TO 39
      DCAN=(PCAN/MXGRO)*CHOAVL
      GO TO 301
   39 DCAN=0.
  301 CONTINUE
      ROOT=ROOT+((PROOT/MXGRO)*CHOAVL)
   33 CONTINUE
      TOTAL=SEED+ROOT+TUBR+CAN
      ATRIB(1)=JDAY+1.
      ATRIB(2)=3
      ATRIB(3)=DCAN
      ATRIB(4)=(0.00423*TAIR)-0.032
      CALL FILEM(1)
      ATRIB(1)=JDAY
      ATRIB(2)=5
      CALL FILEM(1)
      RETURN
      END
C
C   THE CANDE SUBROUTINE CALLS FOR THE REDUCTION OF
C   THE CROP CANOPY BASED UPON AERIAL HEAT UNITS
C   ACCUMULATED IN ATRIB(4).
C
      SUBROUTINE CANDE
 /*INCLUDE COMMON
      ATRIB(4)=ATRIB(4)+((0.00423*TAIR)-0.032)
      IF(ATRIB(4).GT.1.2)GO TO 40
      ATRIB(1)=JDAY+1.
      ATRIB(2)=3
      CALL FILEM(1)
      GO TO 45
   40 CAN=CAN-(0.7*ATRIB(3))
   45 CONTINUE
      RETURN
      END
C
C   THE ENDAY SUBROUTINE IS CALLED AFTER EACH DAY'S
C   GROWTH.  HERE, THE DAY SUBROUTINE IS SCHEDULED,
C   THE THREE-DAY AVERAGE PHOTOSYNTHESIS IS CALCUL-
C   ATED, AND BOTH TABULAR AND GRAPHIC OUTPUT ARE
C   PROGRAMMED.
C
      SUBROUTINE ENDAY
 /*INCLUDE COMMON
      ATRIB(1)=JDAY+1.
      ATRIB(2)=4
      CALL FILEM(1)
      PN(1)=PN(2)
      PN(2)=PN(3)
      PN(3)=PNDAY
      PNAVE=(PN(1)+PN(2)+PN(3))/3.
      WRITE(6,500)JDAY,TOTAL,TUBR,DEBUG,PNDAY,CAN,
     1ROOT,SEED
  500 FORMAT('0',F4.0,2(2X,F8.4),3X,F4.0,4(2X,F8.4))
 /*INCLUDE PLOT
      RETURN
      END
 //GO.SYSIN DD *
GEN,K.INGRAM,1,1,4,1980,1*
STA,(5)1*
```

```
SEBAGO GROWTH AND DEVELOPMENT MODEL


LIM,0,0,200,4,1,2000*
PLO,1,JDAY,0,3,0,1,*
VAR,1,1,T,TOTAL,1,1,0,1000,2,C,CANOPY,1,1,0,1000,
3,P,TUBERS,1,1,0,1000*
INI,1,,,68,138*
FIN*
 /*INCLUDE DATA1
 /*INCLUDE DATA2
 /*INCLUDE DATA3
 /*
//STEP2 EXEC CARDLIST
```

```
INPUT TABLES

C
C   GCSE1 AND GCSE2 ARE TABLES CONTAINING GROUND COVER
C   PERCENTAGES FOR SEBAGO PLANTINGS JDAY 33 AND 73,
C   RESPECTIVELY.  THE DURATION FOR GCSE1 IS FROM JDAY
C   68 THRU 138.  THE DURATION FOR GCSE2 IS FROM JDAY
C   96 THRU 151.
C
      DATA GCSE1/0.01,0.88,2.56,6.94,17.5,34.3,46.5,
     A64.7,82.2,85.5,87.2,85.2,82.2,79.45,76.7/
C
      DATA GCSE2/0.01,3.37,8.96,12.1,22.5,30.2,45.,
     A57.5,70.,81.2,78.,70./
C
C   TCAN IS A TABLE CONTAINING THE RELATIVE CANOPY
C   GROWTH RATE FOR TEMPERATURES FROM 0 TO 30 DEG C.
C
      DATA TCAN/0.,0.01,0.04,0.08,0.12,0.18,0.25,
     A0.32,0.39,0.45,0.5,0.51,0.49,0.44,0.34,0./
C
C   TROOT IS A TABLE WHICH CONTAINS RELATIVE ROOT GROWTH
C   RATE VERSUS TEMPERATURE.
C
      DATA TROOT/0.0,0.15,0.196,0.241,0.287,0.372,0.378,
     A0.385,0.389,0.392,0.424,0.428,0.393,0.312,0.16,0./
C
C   TBIZE IS A TABLE CONTAINING THE TUBER INITIATION RATE
C   VERSUS TEMPERATURE.
C
      DATA TBIZE/0.,0.0128,0.0256,0.0384,0.0512,0.064,
     A0.0672,0.064,0.061,0.0504,0.0395,0.029,0.0132,0./
C
C   TUBRGR IS A TABLE OF THE TEMPERATURE RESPONSE OF THE
C   TUBER RELATIVE GROWTH RATE USED IMMEDIATELY AFTER .
C   INITIATION.
C
      DATA TUBRGR/0.0,0.02,0.06,0.13,0.21,0.34,0.37,
     A0.375,0.375,0.37,0.364,0.35,0.33,0.33,0.3,0.2/
C
C   TTUBR IS A TABLE CONTAINING THE TUBER GROWTH RATE
C   TEMPERATURE RESPONSE.  IT IS USED DURING THE LINEAR
C   PHASE OF TUBER GROWTH (THE BULKING PERIOD).
C
      DATA TTUBR/0.0,0.38,1.237,3.454,6.148,10.43,14.,
     A19.7,18.5,17.,16.,15.,13.,11.,9.,7./
C
C   TSEED IS A TABLE CONTAINING THE CARBOHYDRATE AVAILABLE
C   FROM THE SEED-PIECE VERSUS TEMPERATURE.
C
      DATA TSEED/0.,0.2,0.8,1.94,3.22,3.35,3.42,3.42,
     A3.35,3.28,3.22,2.68,1.21,0.27,0./
//STEP3 EXEC CARDLIST
```

```
      COMMON

       COMMON /GCOM1/ ATRIB(25),JEVNT,MFA,MFE(100),MLE(100),
      1MSTOP,NCRDR,NNAPO,NNAPT,NNATR,NNFIL,NNQ(100),NNTRY,
      2NPRNT,PPARM(50,4),TNOW,TTBEG,TTCLR,TTFIN,TTRIB(25),
      3TTSET
       COMMON /GCOM2/ DD(100),DDL(100),DTFUL,DTNOW,ISEES,
      1LFLAG(50),NFLAG,NNEQD,NNEQT,SS(100),SSL(100),TTNEX
       COMMON /GCOM3/ AAERR,DTMAX,DTMIN,DTSAV,IITES,LLERR,
      1LLSAV,LLSEV,RRERR,TTLAS,TTSAV
       COMMON /GCOM4/ DTPLT(10),HHLOW(25),HHWID(25),IICRD,
      1IITAP(10),JJCEL(500),LLABC(25,2),LLABH(25,2),LLABP(11,2),
      2LLABT(25,2),LLPHI(10),LLPLO(10),LLPLT,LLSUP(15),
      3LLSYM(10),MMPTS,NNCEL(25),NNCLT,NNHIS,NNPLT,NNPTS(10),
      4NNSTA,NNVAR(10),PPHI(10),PPLO(10)
       COMMON /GCOM5/ IIEVT,IISED(6),JJBEG,JJCLR,MMNIT,MMON,
      1NNAME(3),NNCFI,NNDAY,NNPT,NNSET,NNPRJ,NNPRM,NNRNS,NNRUN,
      2NNSTR,NNYR,SSEED(6)
       COMMON /GCOM6/ EENQ(100),IINN(100),KKRNK(100),MMAXQ(100),
      1QQTIM(100),SSOBV(25,5),SSTPV(25,6),VVNQ(100)
       COMMON /UCOM1/ GCSE1(15),TCAN(16),TROOT(16),TTUBR(16)
      1,TSEED(15),TUBRGR(16),JDAY,MXGRO,LFPOOL,MNPOOL,MXPOOL,
      2MNTUBR,BULK,PNDAY,PN(3),SEED,CAN,ROOT,TUBR,TOTAL,TINIT,
      3CHOSED,CHOTOT,POOLAV,TSOIL,TAIR,EXTRA,GCSE2(12),TBIZE(14),
      4PNAVE,BULKMN,PTUBR,DEBUG
       REAL JDAY,MXGRO,MNPOOL,MNTUBR,LFPOOL,MXPOOL
       INTEGER BULK
//STEP4 EXEC CARDLIST
```

```
                INITIAL VALUES FOR THE DAY 33 PLANTING

13 FEBRUARY 1980

SEED=49.57
CAN=1.47
ROOT=0.8774
TUBR=0.
TOTAL=51.917
ATRIB(1)=68.
ATRIB(2)=4.
CALL FILEM(1)


INITIAL VALUES FOR THE DAY 73 PLANTING

SEED=35.53
CAN=1.49
ROOT=0.981
TUBR=0.
TOTAL=38.
ATRIB(1)=96.
ATRIB(2)=4.
CALL FILEM(1)


PLOT INPUTS

DIMENSION PLOT(3)
PLOT(1)=TOTAL
PLOT(2)=CAN
PLOT(3)=TUBR
CALL GPLOT (PLOT,JDAY,1)
```

APPENDIX B:

TABLES OF RAW DRY WEIGHT DATA, TUBERS PER SEED-PIECE, INFLORESCENCES PER SEED-PIECE, STEMS PER SEED-PIECE, TOTAL BRANCH PLUS STEM LENGTH PER SEED-PIECE, PERCENT FINAL EMERGENCE, MAXIMUM LEAF AREA INDEX, MAXIMUM PERCENT GROUND COVER, AND THEIR RESPECTIVE ANALYSES OF VARIANCE

Table B-1. Dry weights of seed-pieces, tubers, and crop total by replicates for the Julian Day 33 planting.

Julian Day	Treatment	Rep.	Seed-Piece	Total	Tuber
			- - - - -	g/m^2 - - - - - -	
66	M 33	1	58.6	60.2	
		2	60.1	62.5	
		3	56.6	59.0	
	S 33	1	62.5	64.9	
		2	59.0	60.1	
		3	59.8	61.3	
73	M 33	1	34.8	38.9	
		2	32.0	35.2	
		3	36.9	40.7	
	S 33	1	28.4	31.4	
		2	35.3	38.2	
		3	24.9	27.7	
80	M 33	1	34.9	40.8	
		2	29.5	40.0	
		3	31.5	40.9	
		4	31.4	40.0	
	S 33	1	14.4	21.2	
		2	16.5	27.8	
		3	18.3	24.7	
		4	26.4	35.7	
88	M 33	1	18.1	42.0	0.28
		2	18.5	52.6	0.37
		3	16.9	50.5	0.39
		4	28.3	58.4	0.60
	S 33	1	17.2	53.6	0.56
		2	12.8	41.0	0.46
		3	12.9	39.2	0.78
		4	12.1	28.6	0.28
95	M 33	1	16.1	108.0	14.8
		2	25.4	142.0	23.4
		3	27.1	165.0	24.9
		4	27.2	149.0	25.0

(Continued)

Table B-1 - Continued.

95	S 33	1	13.8	112.0	10.0
		2	20.6	144.0	15.0
		3	7.4	73.6	5.4
		4	13.2	127.0	9.6
102	M 33	1		182.0	48.5
		2		216.0	65.2
		3		283.0	76.0
		4		260.0	75.1
	M 33	1		287.0	34.6
		2		246.0	42.7
		3		301.0	39.9
		4		231.0	30.1
111	M 33	1		367.0	173.0
		2		420.0	275.0
		3		422.0	218.0
		4		358.0	173.0
	S 33	1		422.0	123.0
		2		376.0	127.0
		3		406.0	131.0
		4		280.0	88.6
121	M 33	1		536.0	319.0
		2		552.0	352.0
		3		564.0	356.0
		4		612.0	396.0
	S 33	1		563.0	238.0
		2		539.0	259.0
		3		582.0	374.0
		4		404.0	170.0
130	M 33	1		643.0	455.0
		2		850.0	608.0
		3		723.0	534.0
		4		754.0	566.0
	S 33	1		643.0	385.0
		2		632.0	386.0
		3		701.0	452.0
		4		747.0	743.0

(Continued)

Table B-1 - Continued.

139	M 33	1	905.0	563.0
		2	979.0	658.0
		3	943.0	591.0
		4	809.0	605.0
	S 33	1	872.0	512.0
		2	828.0	503.0
		3	879.0	498.0
		4	859.0	504.0

Table B-2. Dry weights of seed-pieces, tubers, and crop total by replicates for the Julian Day 73 planting.

Julian Day	Treatment	Rep.	Seed-Piece	Total	Tuber
			- - - - - - g/m^2 - - - - - -		
95	M 73	1	27.7	33.6	
	S 73	1	35.8	38.3	
100	M 73	1	23.6	28.3	
		2	20.8	29.7	
		3	18.9	25.7	
		4	20.3	27.5	
	S 73	1	35.1	39.6	
		2	30.9	35.8	
		3	30.9	34.0	
		4	34.8	38.8	
107	M 73	1	22.9	40.1	
		2	16.5	63.2	
		3	28.9	53.7	
		4	28.3	45.0	
	S 73	1	43.6	53.7	
		2	16.9	33.1	
		3	26.6	36.7	
		4	35.6	59.8	
116	M 73	1	16.1	87.4	18.0
		2	19.9	94.1	22.2
		3	17.7	94.7	19.8
		4	15.1	78.8	16.9
	S 73	1	10.6	71.7	3.93
		2	11.9	81.4	4.42
		3	8.8	73.9	3.27
		4	5.8	56.5	2.16
125	M 73	1		160.0	58.1
		2		174.0	71.5
		3		167.0	58.9
		4		149.0	58.8
	S 73	1		113.0	21.6
		2		89.0	12.5
		3		105.0	20.0
		4		90.8	11.9

(Continued)

Table B-2 - Continued.

139	M 73	1	387.0	223.0
		2	402.0	224.0
		3	400.0	242.0
		4	410.0	229.0
	S 73	1	386.0	118.0
		2	289.0	85.4
		3	268.0	80.6
		4	301.0	96.1
153	M 73	1	412.0	299.0
		2	539.0	399.0
		3	433.0	345.0
		4	485.0	360.0
	S 73	1	584.0	251.0
		2	537.0	242.0
		3	396.0	152.0
		4	519.0	194.0

Table B-3. ANOVA for total crop yields at final harvest.

Source	df	SS	F
Reps	3	8498	NS
Planting (A)	1	627660	124 **
Error (a)	3	15157	
Whole-Unit		651315	
Variety (B)	1	60	NS
A·B	1	8327	2.18
Error (b)	6	22913	
Total	15	682614	

Table B-4. ANOVA for tuber yields at final harvest.

Source	df	SS	F
Reps	3	6638	8.05 **
Planting (A)	1	300304	1093 **
Error (a)	3	824	
Whole-Unit		307766	
Variety (B)	1	58081	39 **
A·B	1	1681	1.1 (NS)
Error (b)	6	8888	
Total	15	376383	

*, **: α - level equal 0.05 and 0.01, respectively.

Table B-5. Number of tubers per seed-piece. Average of all harvests after the full tuber load was achieved.

Planting Day	Rep.	Monona	Sebago
33	1	12.8	6.81
	2	10.3	10.9
	3	11.9	11.0
	4	11.5	8.33
73	1	15.0	10.5
	2	12.0	8.5
	3	16.0	19.5
	4	11.0	6.5

Table B-6. ANOVA for number of tubers per seed-piece in TABLE B-5.

Source	df	SS	F
Reps	3	62	1.77 (NS)
Planting (A)	1	15	1.28 (NS)
Error (a)	3	35	
Whole-Unit		112	
Variety (B)	1	21	3.18 (NS)
A.B	1	0.01	NS
Error (b)	6	40	
Total	15	173	

Table B-7. Number of inflorescences per seed-piece for date of maximum flowering.

Planting Day	Rep.	Monona	Sebago
33	1	1.0	4.7
	2	1.5	7.2
	3	1.5	7.8
	4	1.7	8.7
73	1	0.5	2.5
	2	0.5	1.0
	3	1.5	2.0
	4	1.0	2.5

Table B-8. ANOVA for number of inflorescences per seed-piece in Table B-7.

Source	df	SS	F
Rep	3	4.24	NS
Planting (A)	1	31.67	12.8 *
Error (a)	3	7.4	
Whole-Unit		39.07	
Variety (B)	1	46.14	24.6 **
A·B	1	13.23	7.05 *
Error (b)	6	1.88	
Total	15	109.8	

*,**: α - level equal to 0.05 and 0.01, respectively.

Table B-9. Number of stems per seed-piece. Average of all harvests after full emergence.

Planting Day	Rep.	Monona	Sebago
33	1	1.00	1.33
	2	1.17	1.83
	3	1.17	2.00
	4	1.17	1.50
73	1	4.50	3.25
	2	3.50	1.50
	3	5.00	2.75
	4	3.00	2.25

Table B-10. ANOVA for number of stems per seed-piece in Table B-9.

Source	df	SS	F
Reps	3	1.70	NS
Planting (A)	1	13.29	20.3 *
Error (a)	3	1.96	
Whole-Unit		16.95	
Variety (B)	1	1.05	7.79 *
A·B	1	4.41	32.7 **
Error (b)	6	0.81	
Total	15	23.22	

*, **: α - level equal to 0.05 and 0.01, respectively.

Table B-11. Total stem plus branch lengths per seed-piece at maxima.

Planting Day	Rep.	Monona	Sebago
		- - - - - cm - - - - -	
33	1	148.0	354.0
	2	216.0	402.0
	3	134.0	407.0
	4	202.0	558.0
73	1	71.8	117.0
	2	50.0	44.5
	3	71.4	65.0
	4	95.1	71.8

Table B-12. ANOVA for total stem plus branch lengths per seed-piece in Table B-11.

Source	df	SS	F
Reps	3	10,089	NS
Planting (A)	1	210,314	53.2 **
Error (a)	3	11,866	
Whole-Unit		232,269	
Variety (B)	1	66,435	39.2 **
A·B	1	130,251	76.9 **
Error (b)	6	10,159	
Total	15	372,746	

*, **: α - level equal to 0.05 and 0.01, respectively.

Table B-13. Percent final emergence.

Planting Day	Rep.	Monona	Sebago
33	1	93.8	62.2
	2	100.0	75.0
	3	100.0	75.0
	4	100.0	93.8
73	1	78.8	55.0
	2	88.3	55.3
	3	76.7	46.7
	4	85.0	58.3

Table B-14. ANOVA for emergence percentages in Table B-13.

Source	df	SS	F
Reps	3	330	2.18 (NS)
Planting (A)	1	1554	30.9 **
Error (a)	3	151	
Whole-Unit		2035	
Variety (B)	1	2583	72.2 **
A·B	1	48	1.3 (NS)
Error (b)	6	214	
Total	15	4881	

*, **: α - level equal to 0.05 and 0.01, respectively.

Table B-15. Maximum leaf area index.

Planting Day	Rep.	Monona	Sebago
33	1	1.64	3.70
	2	2.97	3.63
	3	1.90	3.32
	4	3.20	4.00
73	1	0.94	0.94
	2	0.97	0.69
	3	1.25	0.57
	4	1.53	1.22

Table B-16. ANOVA for LAI's in Table B-15.

Source	df	SS	F
Reps	3	1.47	3.31 (NS)
Planting (A)	1	16.49	111.57 **
Error (a)	3	0.44	
Whole-Unit		18.40	
Variety (B)	1	0.84	8.57 *
A·B	1	2.41	24.62 **
Error (b)	6	0.59	
Total	15	22.24	

*, **: α - level equal to 0.05 and 0.01, respectively.

Table B-17. Maximum percent ground cover.

Planting Day	Rep.	Monona	Sebago
33	1	75	95
	2	80	90
	3	85	82
	4	70	70
73	1	70	75
	2	65	90
	3	75	75
	4	85	80

Table B-18. ANOVA for ground cover percents in Table B-17.

Source	df	SS	F
Reps	3	51.2	NS
Planting (A)	1	66.0	NS
Error (a)	3	397.4	
Whole-Unit		496.5	
Variety (B)	1	172.0	2.47 (NS)
A·B	1	0.39	NS
Error (b)	6	418.0	
Total	15	1087.0	

BIOGRAPHICAL SKETCH

Keith T. Ingram was born 18 August 1953 in Corona, California. While his father was in the U. S. Navy, the Ingram family resided in the states of California, Georgia, Florida, and Hawaii.

The author received the Bachelor of Arts degree in psychology from the University of California, Riverside, in June 1974. He was elected to the Phi Beta Kappa Honor Society. In June 1976 he received the Master of Science degree in plant sciences from the same university.

The author enrolled in the Agronomy Department of the University of Florida in September 1976. He expects to receive the degree of Doctor of Philosophy in March 1980 from this institution. He was elected to the Gamma Sigma Delta Honor Society in Agriculture in 1979.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Darrell E. McCloud

D. E. McCloud, Chairman
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

K. J. Boote

K. J. Boote
Associate Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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